THE FINE STRUCTURE OF CRUSTACEAN PROPRIOCEPTORS I. THE CHORDOTONAL ORGANS IN THE LEGS OF THE SHORE CRAB, *CARCINUS MAENAS*

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CONTENTS

In the walking legs of the shore crab, *Carcinus maenas*, is a series of chordotonal organs. Each organ consists of a strand of elastic connective tissue in which are embedded scolopidia. The anatomy and histology of the organs in the coxopodite-basipodite, meropodite-carpopodite, carpopodite-propodite and propodite-dactylopodite joints are described in detail, as seen by light and electron microscopy. The organs are hereafter referred to by the initial letters of the leg segments with which they are associated.

The *CB* organ runs from a projection near the dorsal hinge of the coxa to the dorsal rim of the basipodite. *MC*1 runs from the side of the tendon of the 'accessory flexor' muscle to two attachments on the preaxial wall of the meropodite. *MC*2 runs from the adductor tendon to the preaxial wall of the carpopodite. *CP*1 runs from the productor tendon to two ventral attachments on the carpopodite. *CP*2 runs from the reductor tendon to the floor of the propodite. *PD* runs from the adductor tendon to the postaxial wall of the dactylopodite.

The scolopidia have a tube distal to the scolopale, into which are inserted the ends of the distal processes of bipolar sensory nerve cells. The tube is an extracellular organ apparently formed by the cell that contains the scolopale as an intracellular organ.

Each scolopidium has associated with it two sensory cells, whose cell bodies lie in, on or near the connective tissue strands. In *CB* the sensory cells of a pair are similar to one another (isodynal scolopidia); in the other organs the two cells are dissimilar in their fine structure (heterodynal

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scolopidia). The difference, in the heterodynal scolopidia, consists in the presence or absence of a part of the distal process, the ciliary segment, which has nine double peripheral filaments regularly spaced, and in the precise form of the distal end of the axial filament.

In all scolopidia, the two distal processes of the sensory cells are separated by intrusions of the sheath cells or of the scolopale cell, except for an area near the base of the scolopale where their cell membranes are in apposition; this area is referred to as the ephapse.

At the level of the base of the scolopale the distal processes each contain an axial filament, which shows transverse striations, and there are attachment plaques between the distal processes and the scolopale cell. Distal to this level, each sensory cell contains a centrosome. Distal to the centrosome, the distal processes, which cross the scolopale space to end in the tube, can be divided into the following regions: a ciliary segment (where it occurs), a paraciliary segment characterized by nine double peripheral filaments less regularly arranged than in the ciliary segment, and a terminal segment characterized by numerous single microtubules.

It is suggested that in each scolopidium one sensory cell responds to extension of the strand, and one to its shortening. This might account for the unidirectional responses observed in the organs. No structural basis for the observed differentiation of the sensory cells into 'position' and 'movement' receptors could be found.

Introduction

There has been considerable interest in recent years in proprioceptive mechanisms in invertebrates, particularly in the arthropods. One of the proprioceptor organs described spans the propodite-dactylopodite joint in the walking legs of crabs; it consists of a strand of elastic connective tissue with which is associated a number of bipolar sensory nerve cells (Burke 1954). This organ is only the most distal of a series. Similar structures occur in the other joints of the leg and, in macrurid decapods, across the thoracico-coxal joint as well (Alexandrowicz & Whitear 1957; Alexandrowicz 1958). Wiersma & Boettiger (1959) and Wiersma (1959) continued the investigation of the functions of the organs and confirmed that they are proprioceptive, registering both the position of, and movement in, the joints of the leg. Bush (1962) investigated the reflex connexions of the propodite-dactylopodite and carpopodite-propodite organs.

It has already been reported in a preliminary communication (Whitear 1960*b*), that on investigation with an electron microscope these proprioceptors proved to be chordotonal organs, with the distal processes of the sensory cells inserted into scolopales. Chordotonal organs have been reported from crustaceans on only two previous occasions. Wetzel (1934) described a chordotonal organ from the antenna of *Caprella*, and Barth (1934) found a complex myochordotonal organ in the meropodite of the walking legs of decapods.

The scolopidia contained in the chordotonal organs described in this paper are amphinematic and for the most part heterodynal. As the literature on crustacean chordotonal organs is so scant, it is necessary to turn to that on insects to discuss the terminology. There are two sources of confusion. First, it is not always possible to correlate the results obtained with the electron microscope with those of light microscopy, and secondly, there never has been agreement in the literature as to the terms to be used. As the scolopidia described by Debauche (1935) from the antennae of a trichopteran are evidently comparable to those of the legs of crabs, the terminology used here has been made to correspond, as far as possible, with his, which is also, for the most part, that of Debaisieux (1936). These authors use *scolopidium* to signify a cellular complex enclosing a characteristic element, the *scolopale* (corps scolopal). Usually three cells are involved, of which the most proximal is a sensory cell, but they describe some scolopidia with two sensory cells.

Much of the terminology used springs from the classic paper of Graber (1882). He introduced 'scolopale Körperchen' in place of the usual 'Stifte' or 'Stäbchen' of German authors to avoid possible confusion with the rods of the retina. The term has been anglicized as 'scolopale', which Snodgrass (1935) points out is an adjectival derivative. Graber described the scolopale as hollow and capsular. Comparing his drawings with electronmicrographs of similar material, there can be no doubt of the correspondence of the 'Stifte' to the intracellular organ of fibrous material described as the scolopale in this paper and in the study of the tympanal organ of a locust by Gray (1960). Graber distinguished between *amphinematic* scolopalia which are drawn out into a distal thread, and *mononematic* ones which lack this appendage. Electronmicrographs show that the terminal thread is not precisely a continuation of the scolopale, and is tubular. Nevertheless, the scolopidia described in this paper are clearly amphinematic, while those in the locust's ear are mononematic. (The proximal thread of Graber's description is, presumably, the axial filament, which is within the sensory cell and not part of the scolopale.)

Graber also distinguished between 'integumental' and 'subintegumental' scolopophores. He introduced the term *chordotonal organ*, defining this in the wide sense as including all those sense organs that contain scolopales, but more narrowly as those that have the mechanical property of being under tension like a stretched string. Because Graber thought that this mechanical property related to the reception of sound stimuli, some authors have rejected the term, preferring to use 'scoloparium' (Debauche 1935) or 'scolopophorous organ' (Snodgrass 1935) instead. Snodgrass had previously (1926) objected to the use of 'scolopophorous organ' on the grounds that not all sense organs containing scolopalia could be classified as chordotonal organs. Imms (1957) equates 'scolopophore' with 'scolopidium' and 'chordotonal organs' with 'scoloparia'. Wigglesworth (1953) equates 'scolopidium' with 'chordotonal sensillum'. In the present paper it is considered that *chordotonal organ* is the correct term for sense organs containing integumental scolopophores, where the scolopidia are associated with a connective tissue strand having a distal attachment to the exoskeleton, so that it is under a longitudinal tension. This usage has the advantages of euphony and clarity, because it avoids building further on the root σκόλοψ. It is considered that the question of function is not relevant.

Cohen & Dijkgraaf (1961) call the decapod leg chordotonal organs 'elastic receptors', but this may lead to confusion with the innervated elastic strands at the bases of the legs (Alexandrowicz & Whitear 1957) which are not chordotonal organs (Whitear 1960*b*, and unpublished observations). Pringle (1961) classifies the scolopidial sensory cells as type I arthropod proprioceptors, and the innervated elastic strands as of type II.

Debauche (1935) was the first to describe scolopidia with two sensory cells. In some of these, which he called 'isodynaux', the two sensory cells were similar in structure and position; in others, distinguished as 'heterodynaux', the two cells were dissimilar. The terms isodynal and heterodynal are adopted here, but this does not imply that all the details of structure are the same as in the insect scolopidia Debauche described.

There has been some confusion in the literature as to the use of the terms tendon and apodeme for the skeletal structures to which arthropod muscles attach. Here, tendon is used for the skeletal ingrowth which provides the distal attachment of a muscle.

Material and methods

Fully grown shore crabs, *Carcinus maenas* (L.), were used, usually male. Legs which showed signs of having regenerated were avoided, otherwise specimens were taken from left and right peraeopods II, III, IV and V.

Material to be examined in the electron microscope was fixed in osmium tetroxide. The leg was opened dorsally and the organs exposed by cutting out or laying aside the muscles and the main leg nerve. Cold 2% osmium tetroxide in distilled water was dropped on the organ directly, and a short part of the leg with the organ still *in situ* was quickly transferred to a bath of equal parts of 2% osmium tetroxide and sea water, kept on ice.

It was desirable to know the degree of stretch of the organs on fixation, but unfortunately the elastic strand contracted when the fixative reached it, and was often subsequently stretched again as the fixative reached the muscles still attached to the tendons. The initial shortening alone would be sufficient to prevent one knowing the precise state of the nerve endings at the moment of their fixation.

After 3 h in the cold fixative, the specimen was washed in distilled water, and the organ dissected out, extended in a watch glass, and flooded with absolute ethyl alcohol. Dehydration was in three changes of absolute alcohol, one bath of which contained 1% of phosphotungstic acid; optimum results were obtained if the staining with *PTA* lasted about 50 min. The specimens were embedded in Araldite epoxy-resin (Glauert & Glauert, 1958). Sections were cut on a Porter–Blum microtome with a glass knife, and treated with chloroform vapour to flatten them (Sotelo 1957). As far as possible, serial sections were used; the order of the sections was reconstructed from the prints. The microscope was a Siemen's Elmiskop I.

Because it was necessary to work with serial sections, the process of examination by the electron microscope was laborious and slow, so the total number of specimens examined was not large. Wiersma's results (1959) suggest that there may be variation between animals; therefore the total number of specimens of each organ used is recorded in an appendix.

Histological preparations were stained *supra-vitam* by immersing dissected limbs in a weak solution of methylene blue, made by adding drops of a 0·5% solution of the dye in distilled water, to sea water. The stain was made permanent by treatment with 8% ammonium molybdate, and the specimens mounted in dammar-xylol after dehydration in absolute ethyl alcohol. A few specimens were fixed in Bouin's fluid or in mercuric formol and wax sections stained with Azan or with Heidenhain's iron haematoxylin.

Anatomical preparations were made by fixing the legs in Bouin's fluid. They were washed in 50% alcohol and dissected under water. During dissection, the leg was dipped from time to time in a dilute solution of Chlorazol Black E, which blackened the surfaces, particularly of membranes, and made further dissection easier.

Microscopic anatomy

The anatomy of the chordotonal organ across the propodite-dactylopodite joint was described by Burke (1954) and of that across the coxopodite-basipodite joint by Alexandrowicz & Whitear (1957); nevertheless, these organs will be included in the description

below, for the sake of comparison and completeness. The remaining chordotonal organs have not yet been described adequately. All the organs will be referred to by the initial letters of the leg segments with which they are associated, as has been the practice in the literature since 1957. Figures 1, 2, 4, 6 and 9 were all drawn from the second left peraeopod; the orientation of the leg in individual drawings differs because the view which showed the particular organs to best advantage was chosen in each case. The descriptions apply also to the other walking legs, and to the chelipeds (peraeopods I) if allowance is made for differences of proportion. The nomenclature of the muscles follows that of Cochran (1935) which

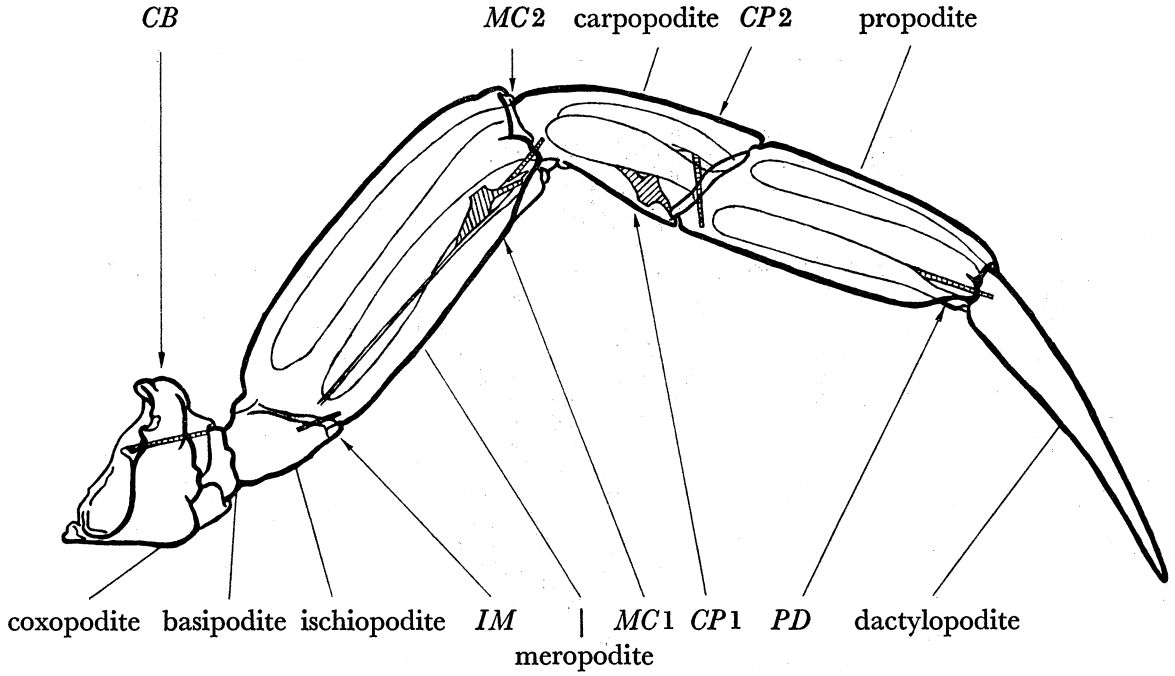


FIGURE 1. Second left peraeopod of *Carcinus maenas* seen from in front, with the positions of the larger tendons and of the chordotonal organs indicated as they would be seen by transparency. (Approx. × 2.)

is also used by Balss (1941). The anatomical drawings were made after all soft parts except the chordotonal organs and the nerves had been dissected away from the skeleton. In some animals the connective tissue strands of the chordotonal organs were firmly attached to the exoskeleton, in others not. This presumably reflects individual differences related to the moulting cycle.

Figure 1 indicates diagrammatically the positions of all the leg chordotonal organs except Barth's organ, as they would be seen by transparency in an anterior view. The ischiopodite-meropodite organ lies across the junction of those two segments, and contains bipolar nerve cells. It is not yet known if it has scolopales. The proximal cranial branch of Barth's three-rayed ligament connects with *IM* across the leg. Barth mentions a nerve in this region, but it is not clear from his description whether the nerve is that of *IM*, or not. The strand of *IM* extends distally past the junction with the ligament to the floor of the meropodite. The examination of this complex with the electron microscope has been deferred, and it will not be mentioned further at present.

Coxopodite-basipodite organ

This organ differs from the more distal chordotonal organs of the leg in that it is not attached to a muscle tendon. It is situated dorsally in the coxopodite. Figure 2 shows it as it appears when dissected from the ventral side. It can be found by pressing apart the anterior and posterior levator muscles. A strand of elastic connective tissue stretches from a peg on the upper rim of the coxa, just anterior to the dorsal hinge, to a point on the dorsal rim of the basipodite between the tendons of the anterior and posterior levator muscles. The distal end of the strand may fray out somewhat.

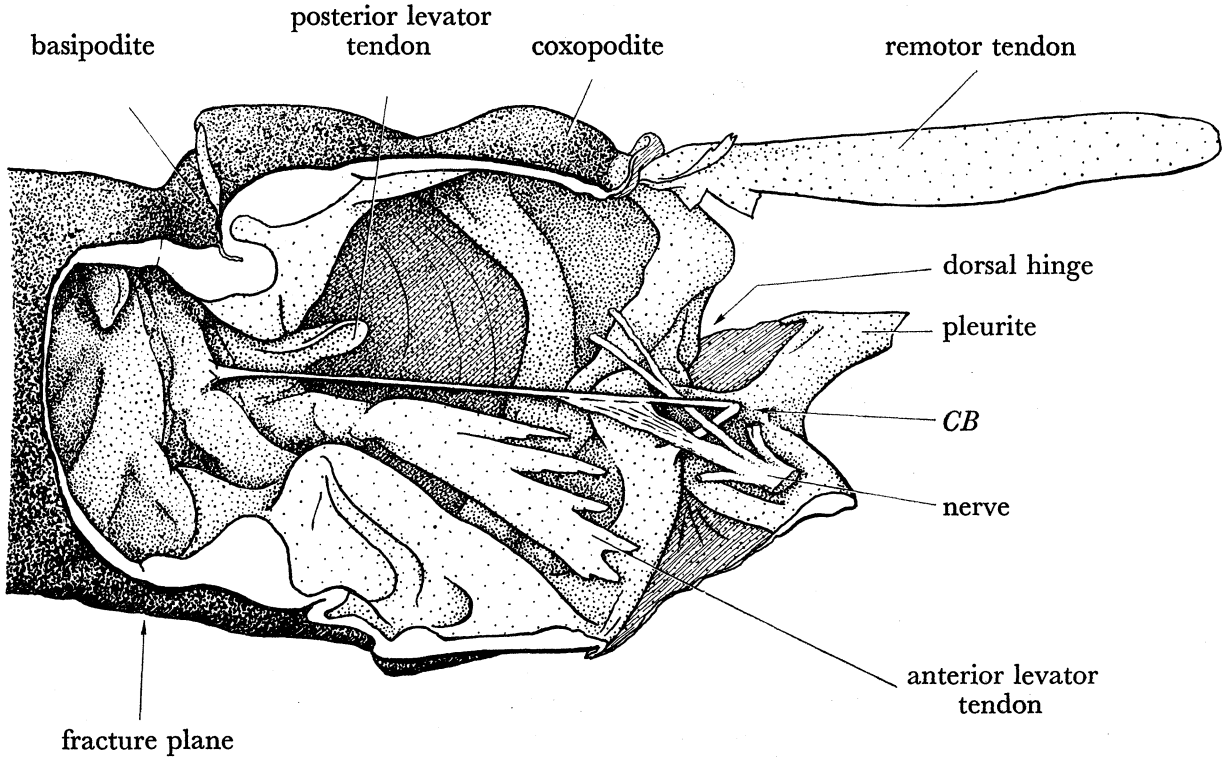


FIGURE 2. Coxopodite of left second peraeopod of *Carcinus maenas* dissected from below. The promotor tendon has been removed. (Approx. × 10.)

The bipolar sensory cells of the organ occur in two groups, not sharply differentiated. The larger, proximal cell bodies lie in, on or near the strand at some distance from its proximal attachment. The more distal cells, which are smaller, lie in or on the strand from the point at which the proximal group ends to a considerable distance distally. The distinction between the two groups of cells is not clear-cut, but the axons of the distal group generally form a bundle rather separate from those of the proximal group, as in figure 3. The nerve as a whole is flattened and strap-like. Soon after leaving the strand it is joined by a number of nerves from the hypodermis of the coxa and of the pleurite. One of the postaxial bundles runs between the proximal part of the elastic strand of *CB* and the peg to which the strand is attached. The stumps of these nerves are shown in figure 2. More proximally, in the thorax, the nerve of *CB* and these various hypodermal branches is joined by another bundle, composed of the 'ganglionated strand' mentioned by Alexandrowicz & Whitear (1957) and bundles from the ventral hypodermis of the coxa. Three

more bundles join the nerve before it eventually runs into the dorsal side of the main leg nerve, well into the thorax.

Electronmicrographs showed that the distal processes of the sensory cells were always associated in pairs. Even in methylene-blue preparations it was occasionally possible to see this. An example is indicated in figure 3, where the cell bodies of the cells concerned also lie side by side. There are seventy-six cells shown in figure 3, but this does not include all the distal cells in the strand, and there may be others, not stained, in the part shown.

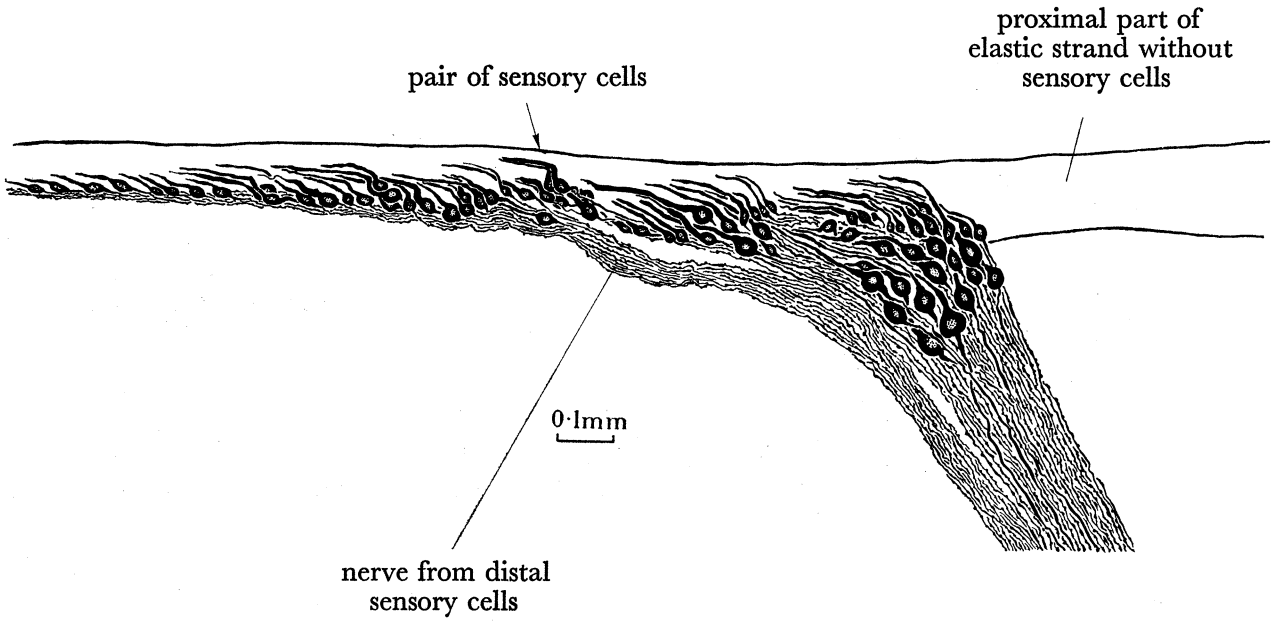


FIGURE 3. Methylene-blue preparation of the *CB* chordotonal organ of *Carcinus maenas*. The most distal part of the strand is omitted.

Meropodite-carpopodite organs

The situation in the meropodite is complicated by the presence of Barth's organ and its associated muscles and tendon. The musculus abductor carpopoditis lies dorsally in the meropodite but attaches more to the preaxial than to the postaxial wall. The musculus adductor carpopoditis attaches ventrally but mostly to the postaxial wall. Between the tendon of the musculus adductor and the preaxial wall of the leg is another, narrow, tendon which is the tendon of the small flexor muscle of Barth (1934) or accessory flexor muscle of Wiersma (1959). It will be referred to here as the accessory tendon. The accessory flexor muscle itself originates on the postaxial wall of the meropodite, proximally; the accessory tendon runs as a thin rod through the length of the meropodite, crossing over to the preaxial side. At the distal end it is broader and flatter and lies alongside the adductor tendon. A membrane extends between the two tendons here, as shown in figure 4. A slip of muscle is inserted on the flattened part of the accessory tendon; it extends obliquely upwards, between the fibres of the musculus abductor, and originates on the preaxial wall about one-quarter of the length of the meropodite from its distal hinge.

The *MC*1 chordotonal organ lies between the preaxial wall of the meropodite and the flattened part of the accessory tendon. It can be found by removing the abductor muscle and the slip of muscle mentioned above. The organ consists of a sheet of connective tissue

with attachments to the accessory tendon and to the wall of the leg; it narrows distally to a strand which is inserted on the rim of the meropodite. The relationships are shown in figure 4. It is easier to describe the spatial arrangements within the sheet if it is referred to the axis of the leg rather than to that of the animal. Accordingly, the side next the accessory tendon will be called mesial, and the side next the preaxial wall, lateral.

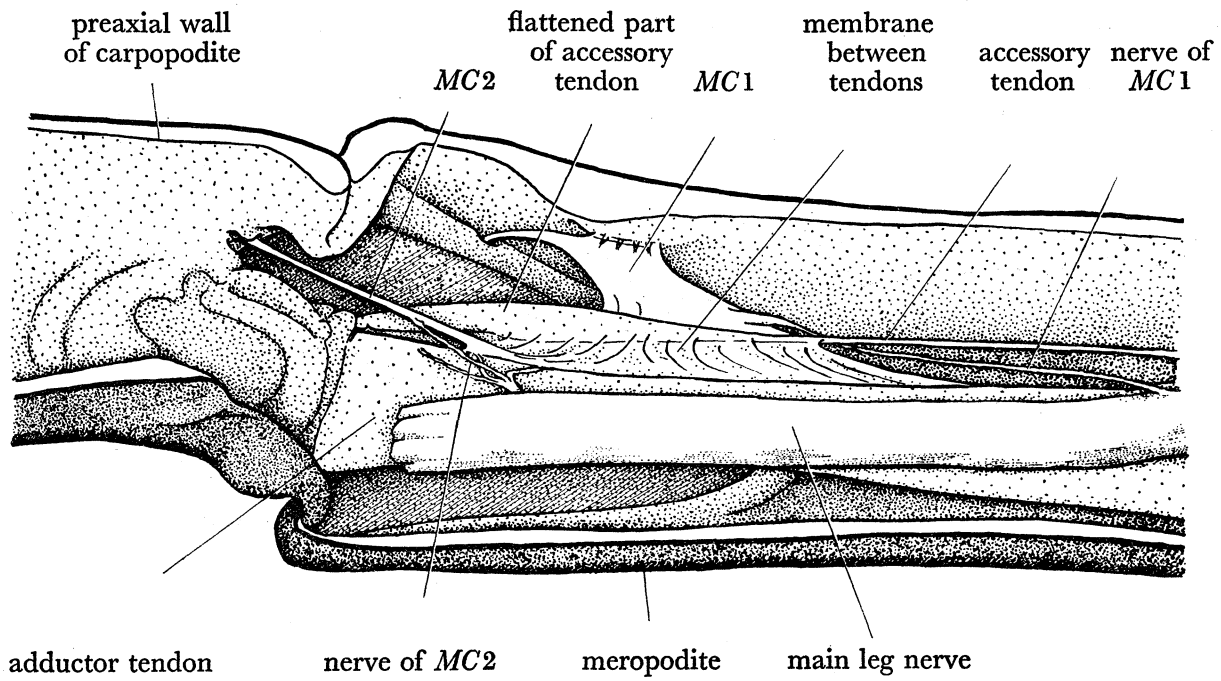


FIGURE 4. Meropodite-carpopodite joint of the second left peraeopod of *Carcinus maenas* dissected from above and behind. The main leg nerve has been displaced to the postaxial side. (Approx. × 10.)

The nerve leaving the chordotonal organ passes beneath the accessory tendon and joins the leg nerve about half way along the meropodite. The arrangement of the sensory cells is shown in figure 5; all are embedded in the connective tissue. Though the large cells are proximal and the smaller ones distal, they are more easily distinguished as lateral and mesial groups, respectively. The small sensory cells extend far down the distal, narrow, part of the organ. Their axons form a bundle running along the mesial side of the sheet, where it is joined by the axons of other small cells which lie side by side towards the mesial side of the sheet. When the organ is in the relaxed position, as in figure 5, the distal processes of these cells are bent at an angle, between the cell body and the scolopale. The large sensory cells do not have this bend. They and their scolopales lie in the proximal half of the sheet, lateral to the smaller cells, and their axons form a loose bundle which joins the nerve from the mesial cells. In the methylene-blue preparation from which figure 5 was drawn, the scolopales and their terminal tubes show unusually clearly, and are indicated in the drawing. It will be seen that some of the scolopales of the large sensory cells are actually more distal than those of some of the smaller, mesial, cells. Some of the tubes appear more undulant than others. The connective tissue sheet is drawn as it usually appears after removal from the leg, but *in situ* the lateral attachment to the wall of the meropodite is less

ragged. Seventy-five cells are shown in figure 5, but this does not include the most distal ones.

*MC*2 is shown in figure 4. A rounded connective tissue strand originates on the preaxial edge of the adductor tendon, distal to MC1, and passes to a point on the preaxial wall of the carpopodite, just beyond the hinge. That is, *MC*2 crosses the joint, unlike *MC*1. There are fewer sensory cells than in *MC*1; some of the larger proximal ones have their cell bodies in the nerve near the strand, the rest are arranged along the strand. The nerve runs directly to the ventral side of the leg nerve and is joined by several small nerve bundles from the tendon.

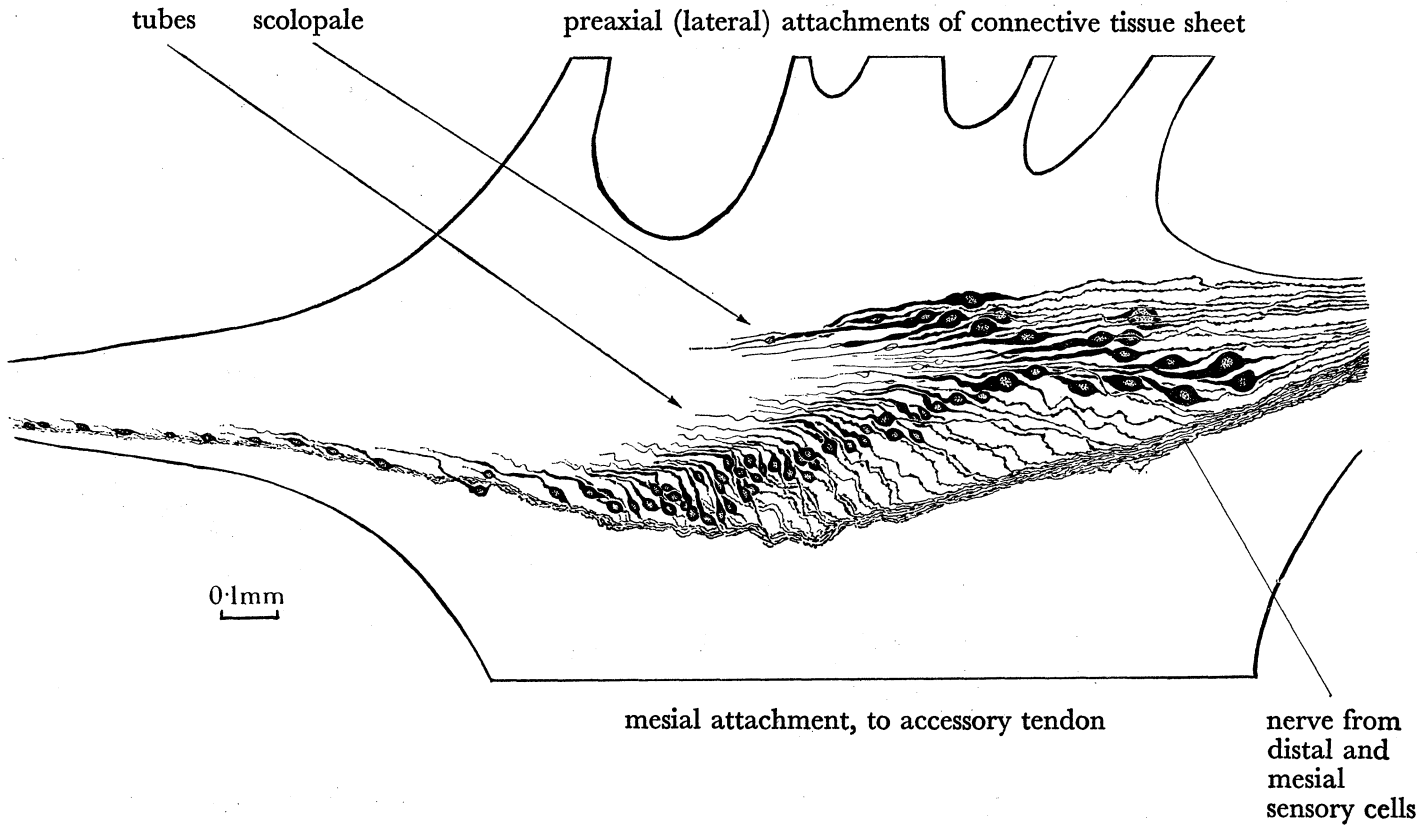


FIGURE 5. Methylene-blue preparation of the *MC*1 chordotonal organ of *Carcinus maenas*. The most distal part of the strand is omitted.

Carpopodite-propodite organs

The *CP* organs resemble the *MC* organs in that one crosses the joint while the other does not, but as they are directly associated with opposing muscles the arrangement is simpler. The organs are shown in figure 6. Both lie ventrally in the leg, and can be exposed by pressing the reductor and productor muscles to either side.

*CP*1 consists of a sheet of connective tissue stretched between the lower edge of the tendon of the musculus productor propoditis and the floor of the carpopodite; it narrows distally to a strand inserted on the ventral rim of the carpopodite preaxial to the mid-line (not to the joint membrane, as is stated by Wiersma 1959). *CP*1 occupies a considerable part of the length of the carpopodite. The nerve leaves it on the mesial side and passes to the preaxial side of the leg nerve, being joined by a small bundle from the ventral hypodermis.

The arrangement of the sensory cells is shown in figure 7; it resembles that of *MC*1, with dorsal and ventral groups of cells in place of the mesial and lateral ones. The bundle of axons from the more distal cells in the strand runs dorsally in the sheet, joined by the axons of the dorsal row of small sensory cells. The large sensory cells are situated proximally and ventrally, all embedded in the connective tissue. In the specimen of figure 7 the size difference of the sensory cells is not so marked as it sometimes is, but it is never an absolute difference. The organ is stretched, so the bend in the distal processes of the dorsal row of cells is not marked. A few scolopales are indicated. Forty-six cells are shown, but this does not include a considerable number in the distal strand, and probably there are more, unstained, in the part drawn.

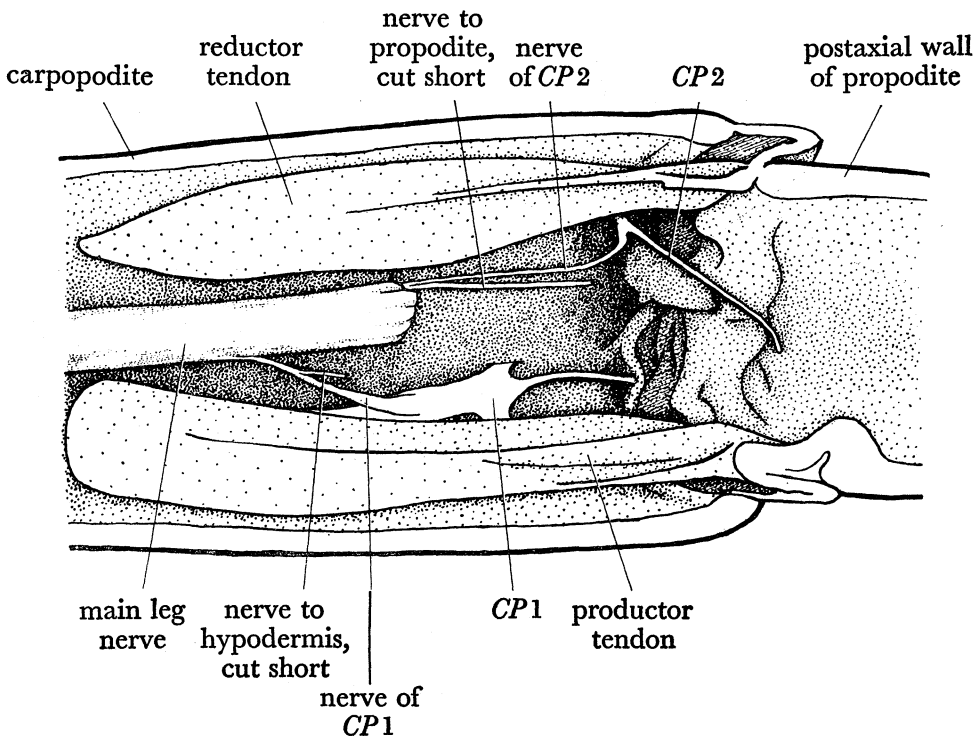


FIGURE 6. Carpopodite-propodite joint of the second left peraeopod of *Carcinus maenas* dissected from above. (Approx. × 10.)

*CP*2 originates on the tendon of the musculus reductor propoditis roughly opposite to the insertion of *CP*1. The rounded elastic strand is attached to the vertical part of the tendon just beneath the horizontal flange, and passes over the hinge to the floor of the propodite. It runs along the proximal edge of a blood channel between the origins of the muscles in the propodite and reaches the exoskeleton just preaxial to the mid-line. The nerve leaves *CP*2 at an angle, due to the position of the organ beneath the reductor tendon. It is joined by a small nerve bundle from the tendon, which is often applied closely to the proximal part of the connective tissue strand. As the nerve from *CP*2 reaches the postaxial side of the leg nerve, about half way along the carpopodite, it is joined below by another, larger, nerve, which is a useful landmark in that it passes into the propodite over the strand of *CP*2, and along the postaxial side of the blood channel mentioned above. This nerve is shown cut short in figure 6. A methylene-blue preparation of the proximal part of

*CP*2 is shown in figure 8. The small distal sensory cells are scattered along the strand, some of the large proximal ones are loosely bound to the nerve. The small nerve bundle running along the proximal part of the strand comes from the tendon. Twenty-three cells are shown in the drawing. Probably the total number of cells is not much higher, for a count of the axons (in electronmicrographs) in the nerve near the strand gave a number of 22; this would have omitted the most proximal cells. There is no reason to suppose that there is a constant number of cells in the organs in different animals, but there are regularly more in *MC*1 and *CP*1 than there are in *MC*2 and *CP*2.

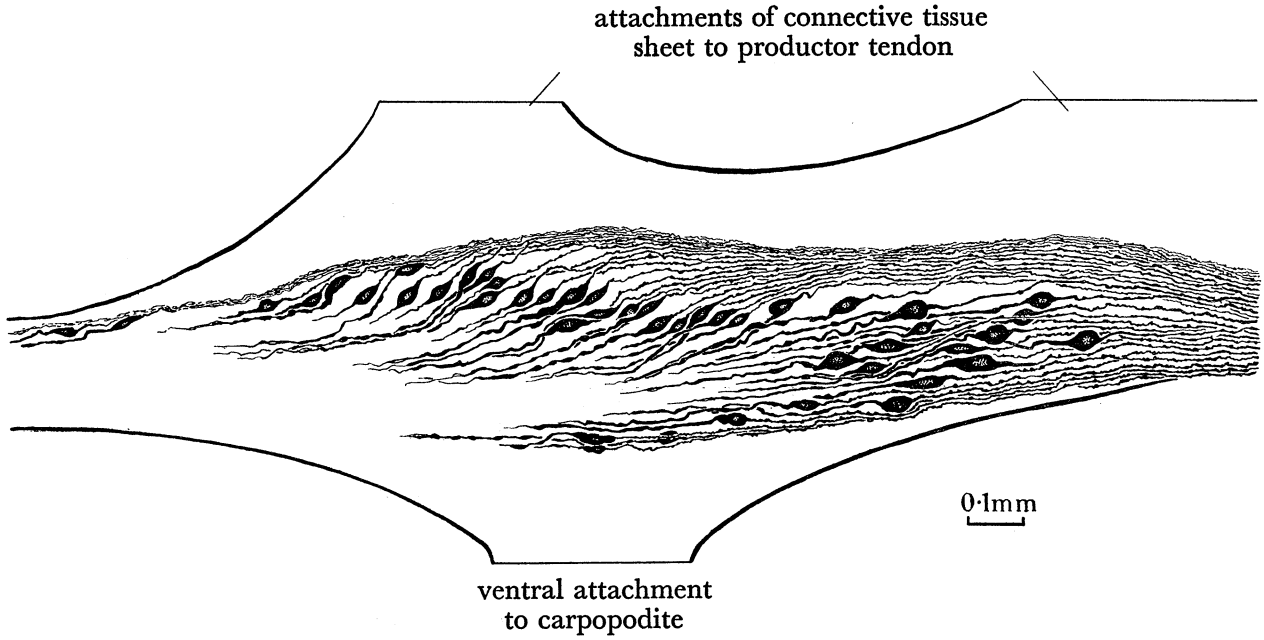


FIGURE 7. Methylene-blue preparation of the *CP*1 chordotonal organ of *Carcinus maenas*. The most distal part of the strand is omitted.

Propodite-dactylopodite organ

The organ is situated ventrally in the leg, and can be exposed by removing the musculus abductor dactylopoditis and displacing the leg nerve to one side. In figure 9 the preaxial wall of the propodite has been cut away. The connective tissue strand extends from the upper ridge of the tendon of the musculus adductor dactylopoditis to a boss on the postaxial wall of the dactylopodite just above the level of the hinge; a few thin strands stretch like guy ropes to the wall of the dactylopodite more proximally. The nerve from the chordotonal organ joins the leg nerve ventrally rather more than half way along the propodite (measuring proximal to distal). A small nerve from the tendon joins the *PD* nerve, passing on one side or the other of the proximal part of the elastic strand. The larger proximal sensory cells of *PD* have their cell bodies in a loose bundle dorsal to the elastic strand. The appearance of the *PD* organ in methylene-blue preparations has been illustrated by Burke (1954).

SUBMICROSCOPIC ANATOMY

The description of the scolopidia is included under this head because they were not discovered until the material was examined by electron microscopy. In insects, many details

of the structure of scolopidia can be seen quite well by light microscopy. In crabs, scolopales can be seen occasionally in methylene-blue preparations, and can be made out, rarely, in sections, but they are so indistinct that they would not be recognized unless they were already known to be present. It is probably because they are embedded in dense

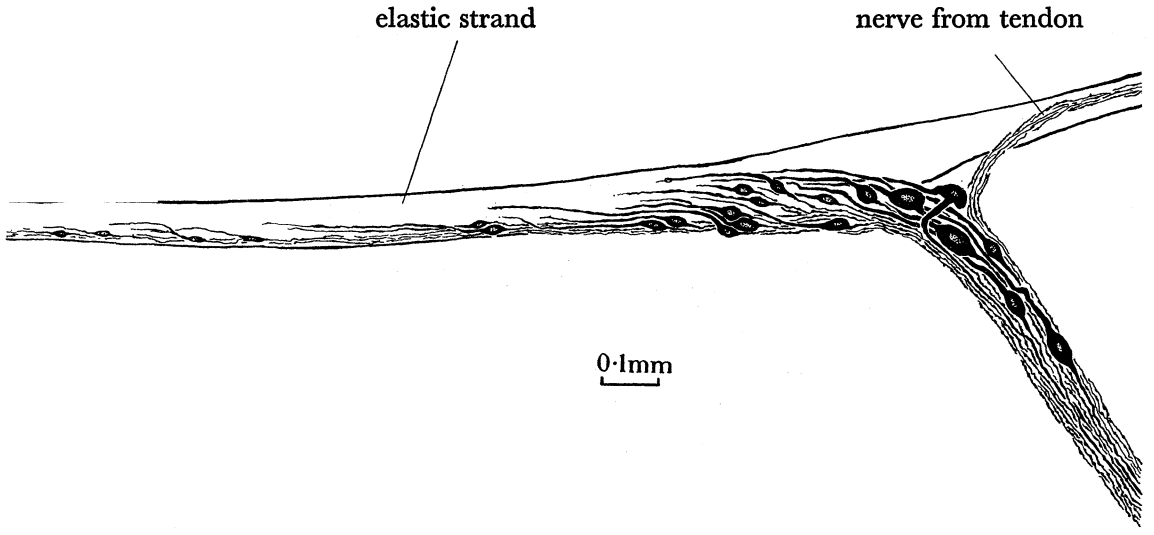


FIGURE 8. Methylene-blue preparation of the *CP*2 chordotonal organ of *Carcinus maenas*. The most distal part of the strand is omitted.

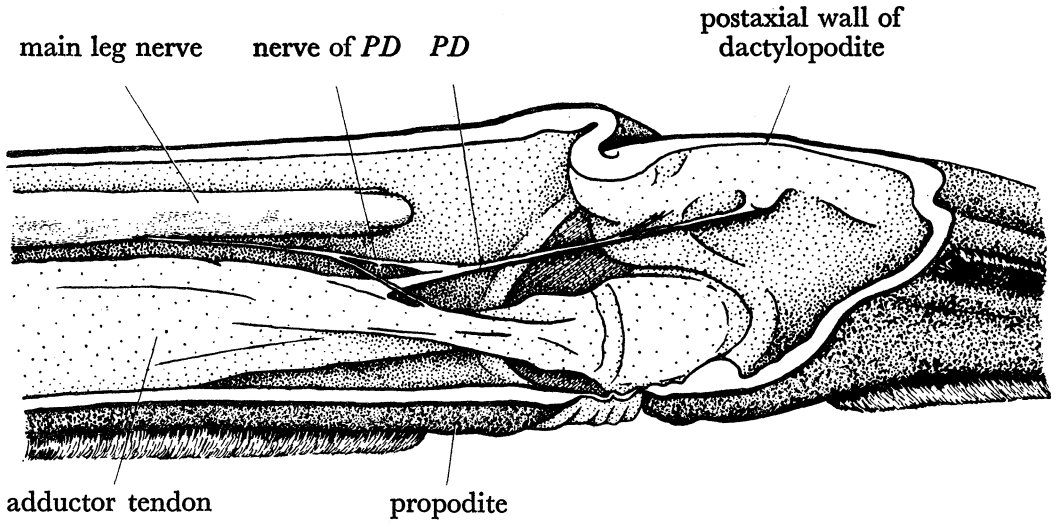


FIGURE 9. Propodite-dactylopodite joint of the second left peraeopod of *Carcinus maenas* dissected from above and in front. (Approx. × 10.)

connective tissue that the crustacean scolopidia are difficult to identify at low magnifications (this does not apply to the scolopidia of Barth's organ).

A brief account of the essential structure of a scolopidium of a crab's leg will be given first, as the basis for a more detailed description of the fine structure of the tissues concerned, and of the variations encountered in the different chordotonal organs. Part of this information has already been published (Whitear 1960*b*) but some details of the preliminary report now need correction.

Each scolopidium has two sensory nerve cells, the perikarya of which may be a considerable distance from the scolopale. The length of the distal process of the proximal sensory cells is usually more than 100 μ, and often as much as 400 μ. For part of this distance the processes lie side by side in the substance of the elastic strand; they are wrapped in sheath cells, which also separate the two distal processes of a pair. It is not clear how many of these sheath cells there are along the length of the distal processes; it may be only one. Figure 10 shows a scolopidium from the proximal part of *CB*; the cell bodies lie just outside the strand. Here only one sheath cell is drawn; the position of its nucleus was reconstructed from electronmicrographs, but the proximal limits of its cytoplasm are not known.

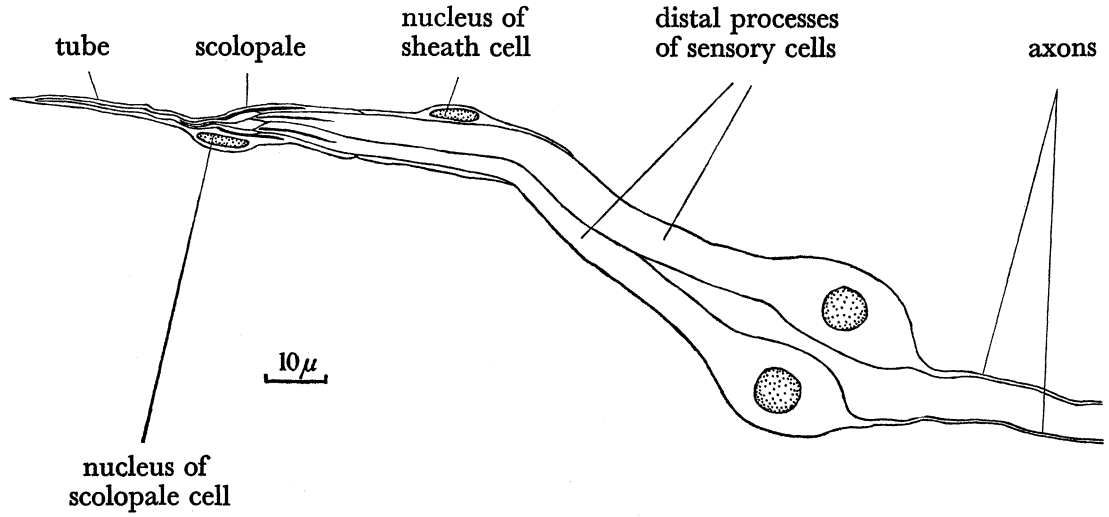


FIGURE 10. Isodynal scolopidium of the *CB* chordotonal organ of *Carcinus maenas*. Based on a camera lucida drawing.

Figure 11 shows details of the structure of scolopidia in diagrammatic reconstructions. The scolopale is a helmet-shaped intracellular organ of fibrous material. It and its associated cytoplasm enclose an extracellular scolopale space. This space is continuous distally with the lumen of a tube which is the 'terminal thread' of amphinematic scolopidia. The proximal part of the hollow of the scolopale is filled by the distal processes of two sensory cells which enter its base. Each distal process contains an axial filament. Within the scolopale the distal processes narrow and run across the scolopale space to enter the lumen of the tube, in which they end. The whole scolopidium (with the exception in some cases of the sensory cell bodies) is enclosed within the connective tissue strand of the chordotonal organ.

Connective tissue

In the elastic strands of the chordotonal organs, and in the mesenteries or membranes supporting the nerves, two types of connective tissue can be distinguished. One is apparently a form of collagen: it consists of long fibres about 200 Å in diameter, which in longitudinal view show cross-striations with a major period of about 500 Å. Collagen is known to be a connective tissue element in crustaceans (Rudall 1955). The second type of connective tissue appears granular but amorphous in both transverse and longitudinal sections. In the elastic strands it occurs chiefly on the periphery. Figure 12, plate 56, shows a portion of

a membrane with collagen fibres and amorphous tissue. Figure 13, plate 56, shows part of an elastic strand with the amorphous tissue on the periphery, and bundles of collagen fibres intermixed with the cytoplasm of connective tissue cells. The nuclei of some connective tissue cells can be seen in the general view of the strand of *CP*1 in figure 29, plate 59. The proportion of extracellular collagen to cell cytoplasm varies in different

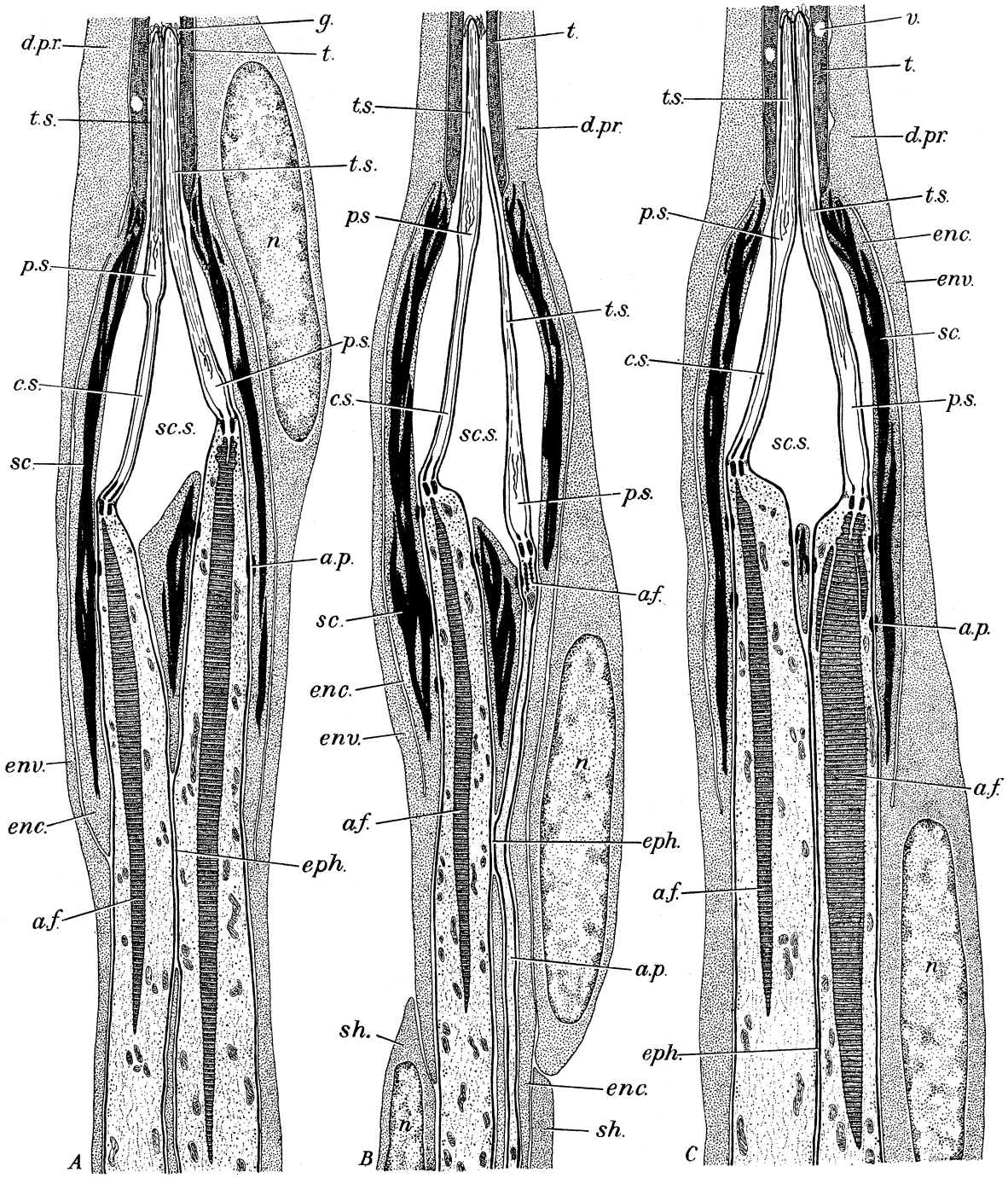


FIGURE 11. Diagram to show the structure of three types of heterodynal scolopidia found in the chordotonal organs of *Carcinus maenas*. *A*, from *PD*. *B*, from *CP*2 or *MC*2. *C*, from *CP*1 or *MC*1. Ciliary sensory cell distal process on the left, and that of paraciliary cell on the right, in each case.

organs and in different parts of the same organ. In wax sections stained with Azan, there was a red sheath on the outside of the strand, which is presumed to correspond to the amorphous connective tissue, while the bulk of the substance of the strand appeared blue with red streaks.

Sheath cells

It has already been mentioned that the distal processes of the sensory cells are wrapped in sheath cells. The axons are similarly covered. Outside the strand, each sensory cell body is covered by several layers of satellite cells and a layer of connective tissue forming a capsule. Cell bodies embedded in the strand lack a special capsule and may have only a thin covering of satellite cells.

The sheath cells must themselves be capable of forming collagen, for collagen fibres are found outside them, and between their projections, in the elastic strand. The same applies to the scolopale cell.

For most of their extent, the distal processes of a pair of sensory cells are separated by a tongue of the sheath cell, which intrudes between them.

The scolopale cell and associated structures

Debaisieux (1936) defined a scolopidium as consisting usually of three cells: a sensory cell proximally, a middle cell which encloses the scolopale, and a distal cell. English authors usually call the middle cell the envelope cell and the distal one the cap cell. In the crab chordotonal organs it is not easy to be sure which are the homologues of these cells and the names have been avoided. The cell that presumably corresponds to the middle or envelope cell has a complicated configuration and in the preliminary report of this work was misinterpreted. The structures referred to by Whitear (1960*b*) as sheath cells, scolopale cell, and tube cells are now thought to be all parts of the same cell, the *scolopale cell.* For technical reasons it is difficult to reconstruct the form of this cell accurately and there is still room for error. There appears, however, to be only one nucleus available for the cytoplasm of all three regions.

The *scolopale* itself is here defined as an agglomeration of fibrous material contained within a special *enclave* of the scolopale cell; it is therefore an intracellular organ. Defined in this way, the scolopale of electron microscopy corresponds to the more important part of the organ as described by light microscopists, and several confusions are avoided, which might prove inconvenient if greater latitude were allowed in the definition. The scolopale cell enclave encloses the extracellular *scolopale space,* which is presumably filled with fluid during life. After fixation the contents appear as scattered flecks and spots or irregular filaments, and can be seen in any section of a scolopale, especially figure 44, plate 62.

The scolopale is helmet shaped in that towards the distal end, or tip, it forms a complete cylinder, but proximally it is better developed on one side than on the other, so that it forms an incomplete cylinder. More proximally still there may be only a series of rods in the scolopale enclave. The walls of the scolopale are not solid, but are formed of bundles of fibrous material more or less interconnected. At intervals these bundles approach and apparently touch the cell membrane that bounds the scolopale space. The cytoplasm in the interstices of the fibrous bundles, and elsewhere in the enclave, contains longitudinal tubules about 200 Å in diameter. There are also various profiles of the endoplasmic

reticulum, but mitochondria are rare. Tubules and other cytoplasmic contents of the enclave show in figure 23, plate 58. The fibrous nature of the scolopale material is brought out by the longitudinal section, figure 44, plate 62. This material is evidently not chitinous, for it bears no resemblance to the substance of the inner layers of the exoskeleton, as seen in sections of tendons or apodemes. In the outer layers of the skeleton there is fibrous material of comparable electron-density, but this is not to say that it is chemically similar.

The enclave of the scolopale cell was at first thought to be a distinct cell. On the outside of the scolopale enclave a 200 to 300 Å gap separates the cell membrane from another, which bounds what was presumed to be the envelope cell of light microscopists. Occasionally the gap is larger, leaving small extracellular spaces, especially towards the tip of the scolopale. The gap and spaces correspond morphologically to the 'extracellular region' of Gray's description (1960) of locust ear scolopidia. No separate nucleus could be found for the cytoplasm around the scolopale. Careful search revealed interruptions in the cell membrane of the enclave both near the extreme tip, and near the base, of the scolopale; at these places the cytoplasm of the scolopale enclave was continuous with that of the supposed envelope cell. An apparent break in a cell membrane may occur where it happens to be cut obliquely, but the cytoplasmic bridges were seen so constantly in the two places mentioned, in both transverse and longitudinal sections, that it seems inescapable that they have a real existence. The part of the scolopale cell that is wrapped around the enclave and extends proximal to it may be called the *enveloping portion.* This contains the nucleus, which may occur at the level of the scolopale-tube junction, or may be proximal to the scolopale, in the region of the axial filaments, or may be in an intermediate position. Mitochondria are especially plentiful near the nucleus. It is difficult to determine the proximal limits of the enveloping portion of the scolopale cell; sometimes, as in figure 11 *B*, the nucleus of the sheath cell was near, or even overlapped, that of the scolopale cell, but usually the sheath cell nucleus was placed more proximally, in the region where the distal processes had not got axial filaments. Figure 36, plate 60, shows the scolopale cell nucleus near the tip of the scolopale, with the walls of the enclave interrupted. Figure 20, plate 57,

Description of plates 56 to 62

Note on plates: the plates have been so arranged that sections from each of the chordotonal organs occur consecutively, with those at proximal levels preceding those which are more distal. With the exception of plate 57, each plate has sections from only one organ. All the figures in the plates are from electronmicrographs of material fixed in osmium tetroxide and stained with *PTA.*

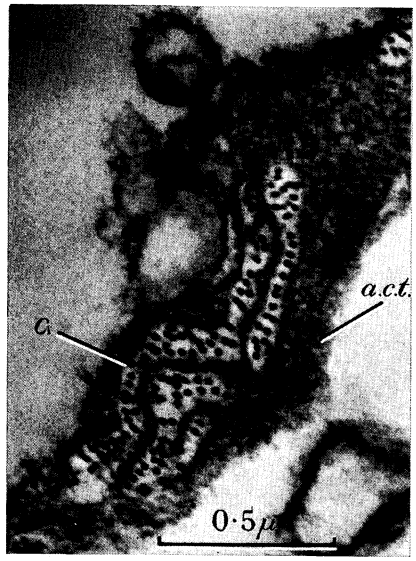
Plate 56

Tranverse sections from *CB* organ.

Figure 12. Part of the membrane supporting the nerve bundle, showing collagen fibres and amorphous connective tissue.

Figure 13. Edge of the elastic strand, proximal to the region with sensory cells. In the body of the strand connective tissue cells are mixed with extracellular bundles of collagen fibres. Amorphous connective tissue appears on the periphery.

Figure 14. Part of the nerve bundle showing axons and sheath cells. Some axons share a sheath cell, others have one each. Collagen fibres appear in the connective tissue sheath of the nerve bundle.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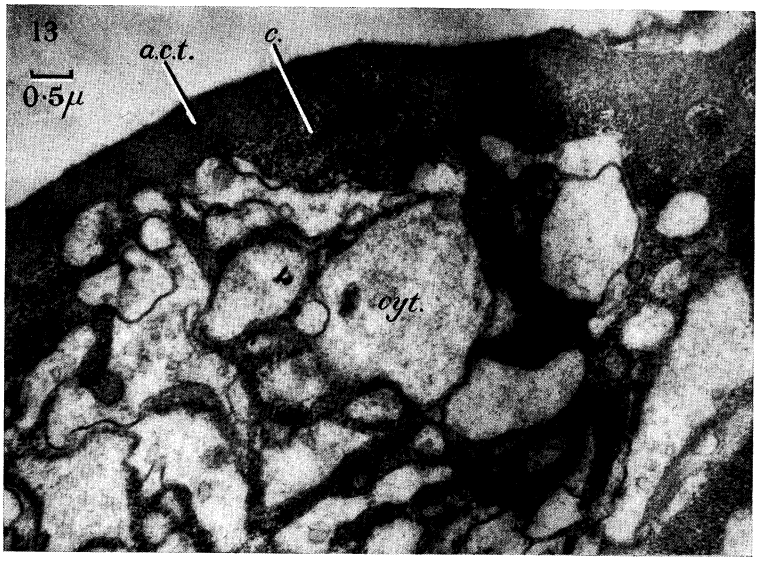
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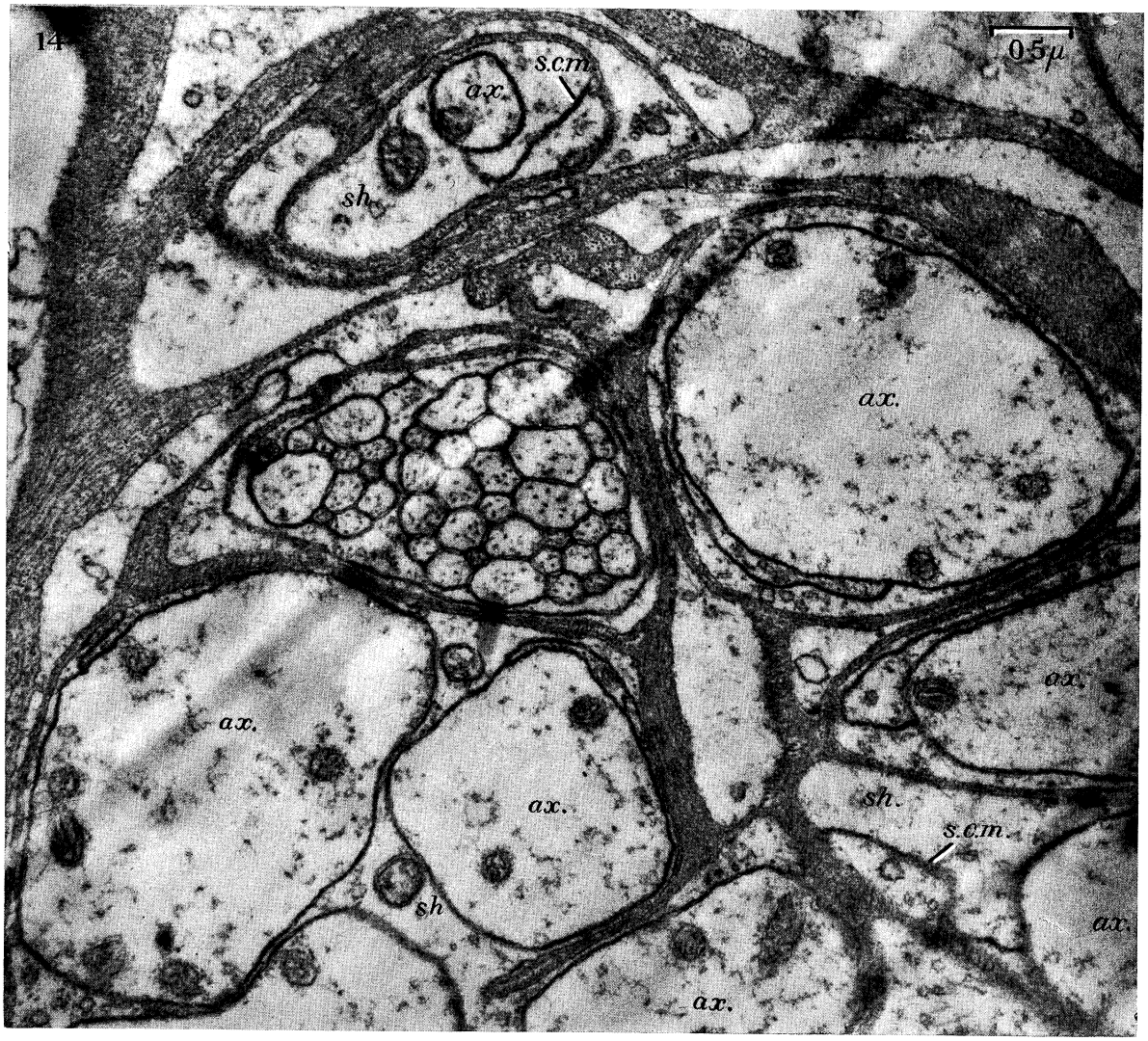
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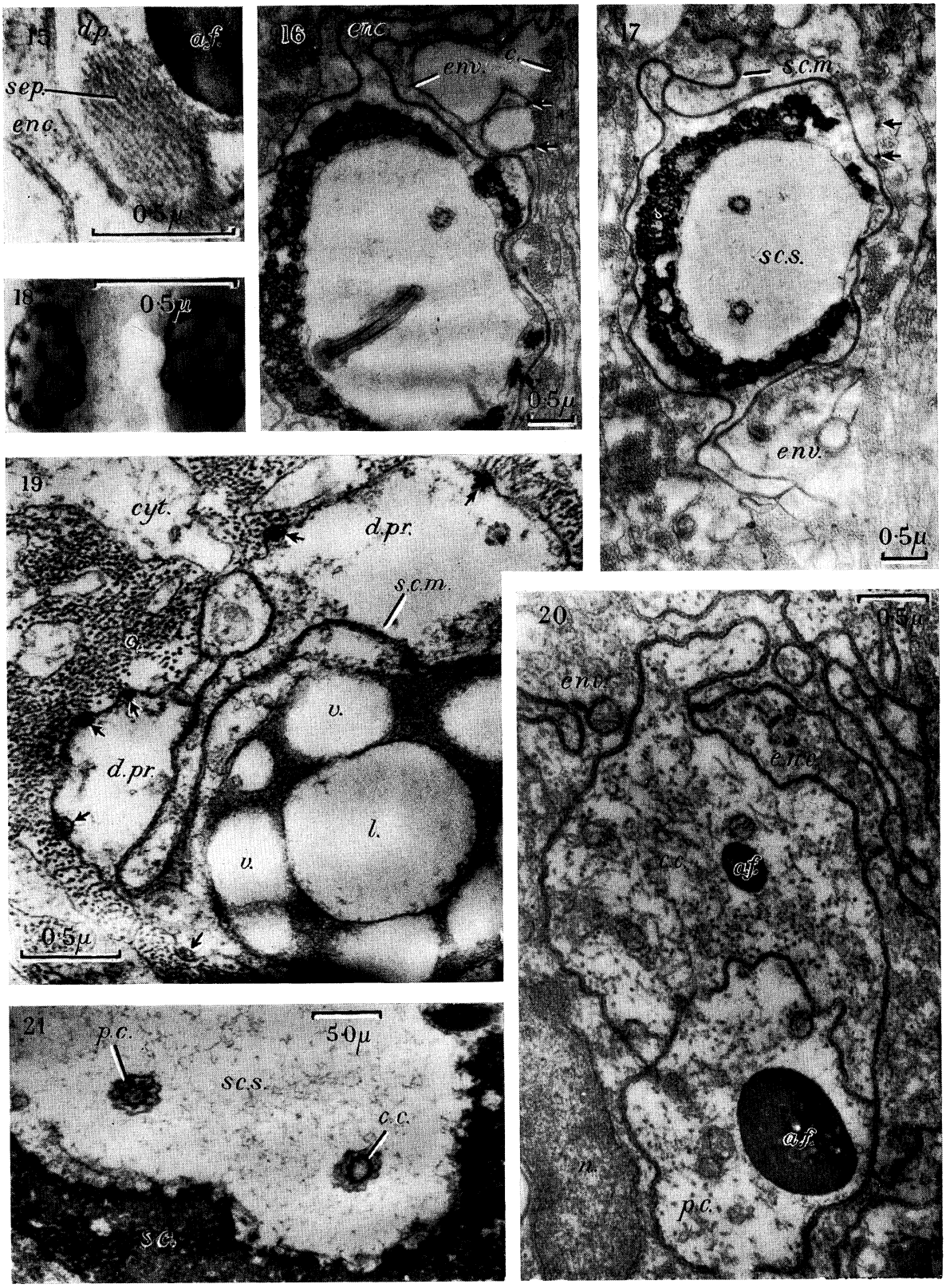
(*Facing p.* 306)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s.c.

Plate 57

Figures 15 to 19, *CB*. Figures 20 and 21, *MC*1. All transverse sections.

Figure 15. Surface view of the septa between the cell membranes of a distal process and the scolopale cell enclave.

Figure 16. Isodynal scolopidium, showing the scolopale and the base of one of the ciliary segments. The two arrows indicate dark bodies on the membrane of the enveloping portion of the scolopale cell, serial to those indicated in figure 17.

Figure 17. Section serial to that of figure 16, showing both ciliary segments. Arrows as in figure 16.

Figure 18. The paraciliary segments in an isodynal scolopidium, each showing nine peripheral filaments and some central filaments.

Figure 19. Tube showing vacuolation of the wall, and one of the two pairs of surface-connecting membranes between the distal prolongations of the scolopale cell. The arrows indicate dark bodies on the cell membranes of the distal prolongations of the scolopale cell.

Figure 20. Heterodynal scolopidium showing the distal processes of the ciliary and the paraciliary sensory cells at the ephapse. The nucleus is that of the scolopale cell.

Figure 21. Heterodynal scolopidium showing the tip of the centriole in the paraciliary cell and the ring at the base of the ciliary segment in the ciliary cell. The scale of this figure has been wrongly labelled. It should read 0·5μ not 5·0μ.

PLATE 58

Transverse sections of *MC*2. Figures 23 to 27 are from a single scolopidium.

FIGURE 22. The two distal processes at the ephapse. The proximal prolongation of the scolopale cell enclave is outside the smaller, paraciliary cell, distal process. The centrosome is that of a sheath cell.

FIGURE 23. Section through a scolopale showing the axial filaments of the sensory cells, that of the paraciliary cell consisting of a few fragments only. The centrosome, at the top of the figure, is that of the scolopale cell. The scolopale enclave shows tubules and other cytoplasmic structures.

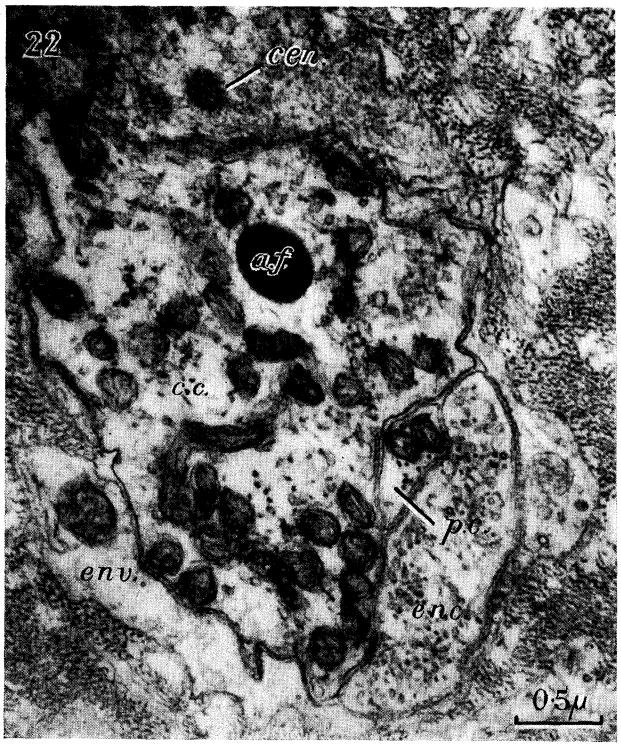
FIGURE 24. Section near the tip of the scolopale showing a break in the terminal segment of the paraciliary sensory cell. The arrow indicates a process from the scolopale cell enclave.

FIGURE 25. Ciliary segment showing the rod and tube arrangement of the nine peripheral filaments.

FIGURE 26. Section serial to that of figure 24, showing the paraciliary segment of the ciliary sensory cell with nine double peripheral filaments and one central filament. The terminal segment of the paraciliary cell is intact again.

FIGURE 27. Tip of scolopale showing the transition between the paraciliary and terminal segments of the ciliary cell; some double peripheral filaments can still be traced (arrowed).

FIGURE 28. Tube, beyond the ends of the distal processes, showing granular material in the lumen, which differs from the 'glue'.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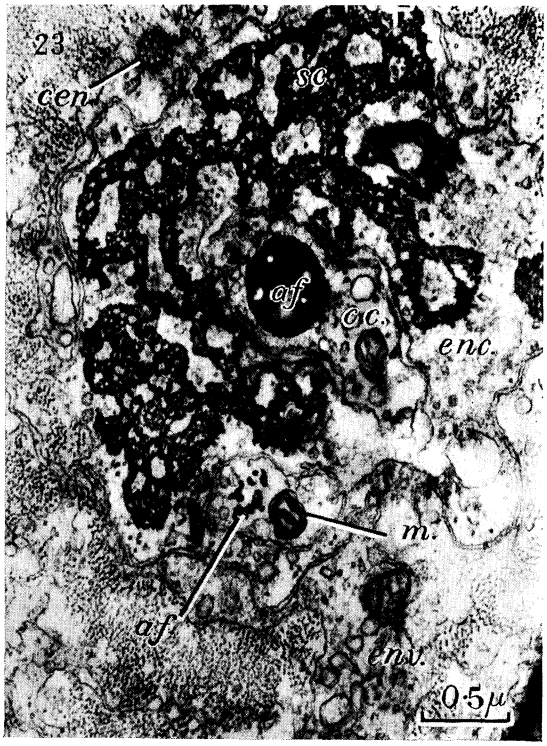
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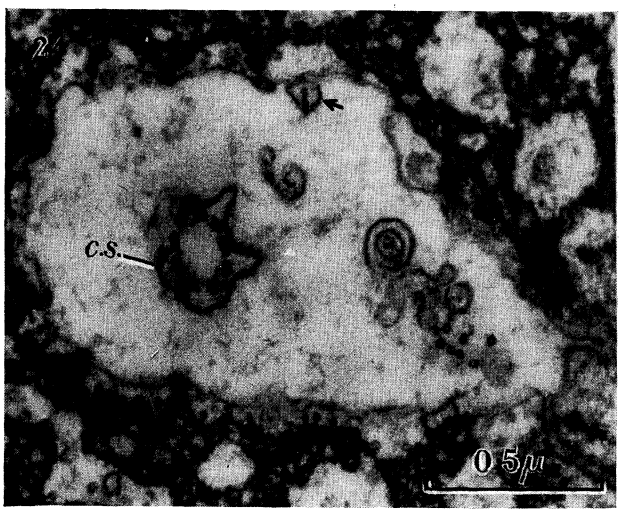
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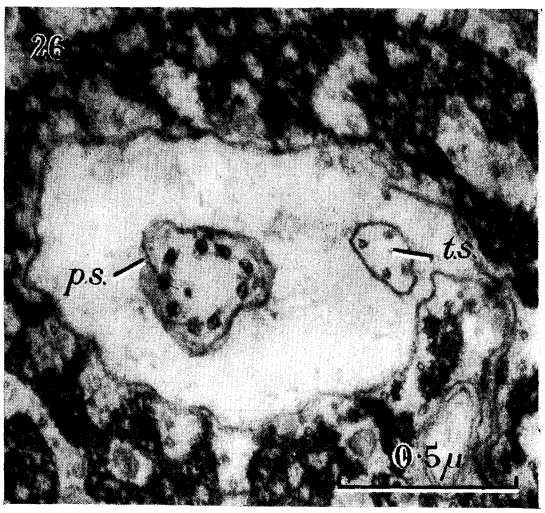
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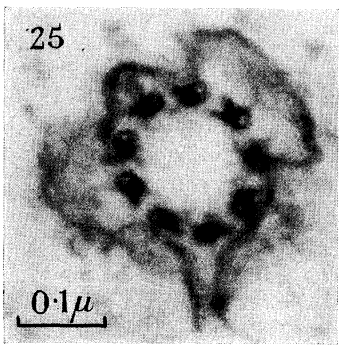
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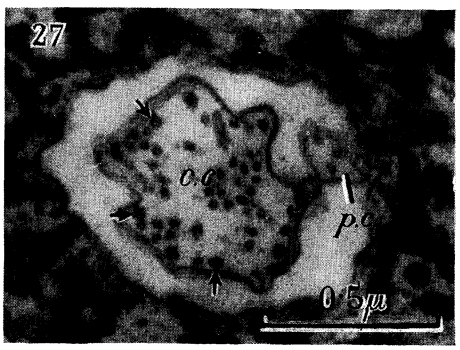
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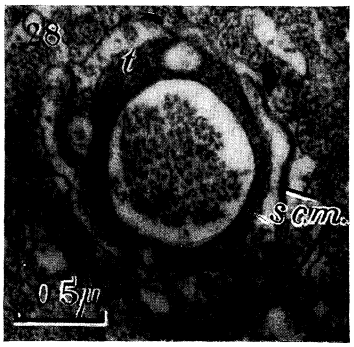
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Plate 59

Sections of *CP* 1, figures 30 and 31 longitudinal, the rest transverse.

Figure 29. Low power view of part of the connective tissue sheet, the edge of which appears at the top of the picture. Scolopidia are cut at various levels; to the right are tubes with the scolopale cell prolongations showing some fibrous material. A scolopale with its nucleus is in the middle, and distal processes of sensory cells, with and without axial filaments, to the left. The remaining nuclei are of connective tissue cells.

Figure 30. Axon showing 'thick' filaments in longitudinal view.

Figure 31. A pair of distal processes showing part of the ephapse (arrowed) in longitudinal view. Mitochondria, filaments and vesicular profiles appear in the cytoplasm of the distal processes.

Figure 32. Transverse section of an ephapse at a level comparable to the upper part of figure 31.

Figure 33. Base of scolopale with the two distal processes containing axial filaments; that of the paraciliary cell is incised, and there are two subsidiary axial filaments (arrowed). There are attachment plaques between the distal processes and the scolopale cell enclave; one of these is arrowed.


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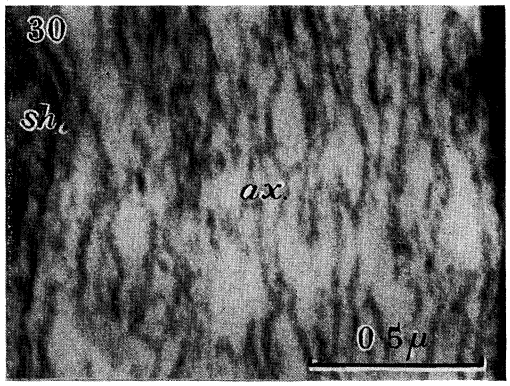
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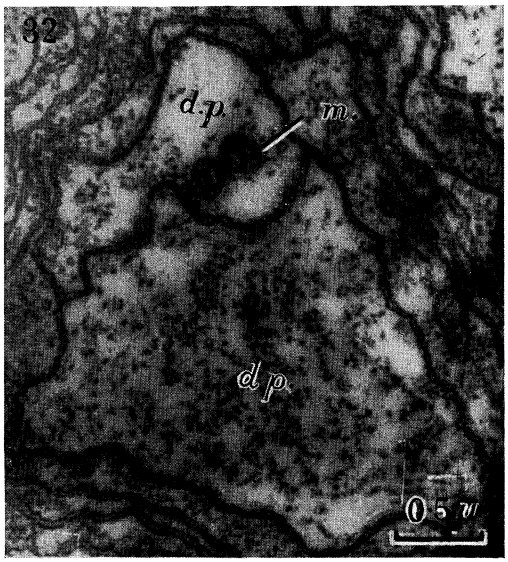
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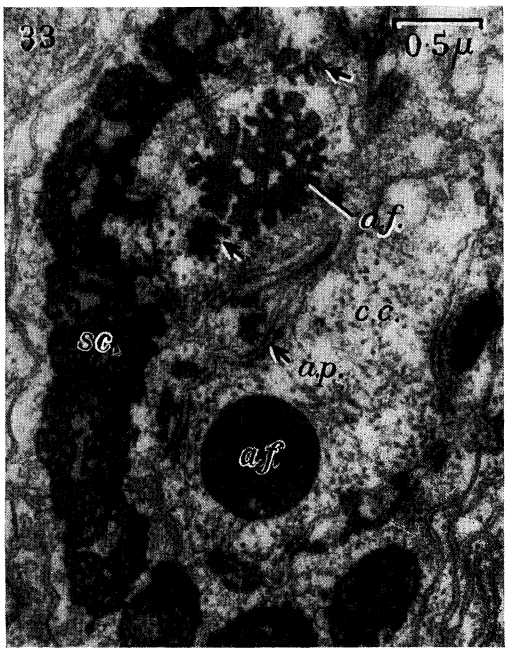
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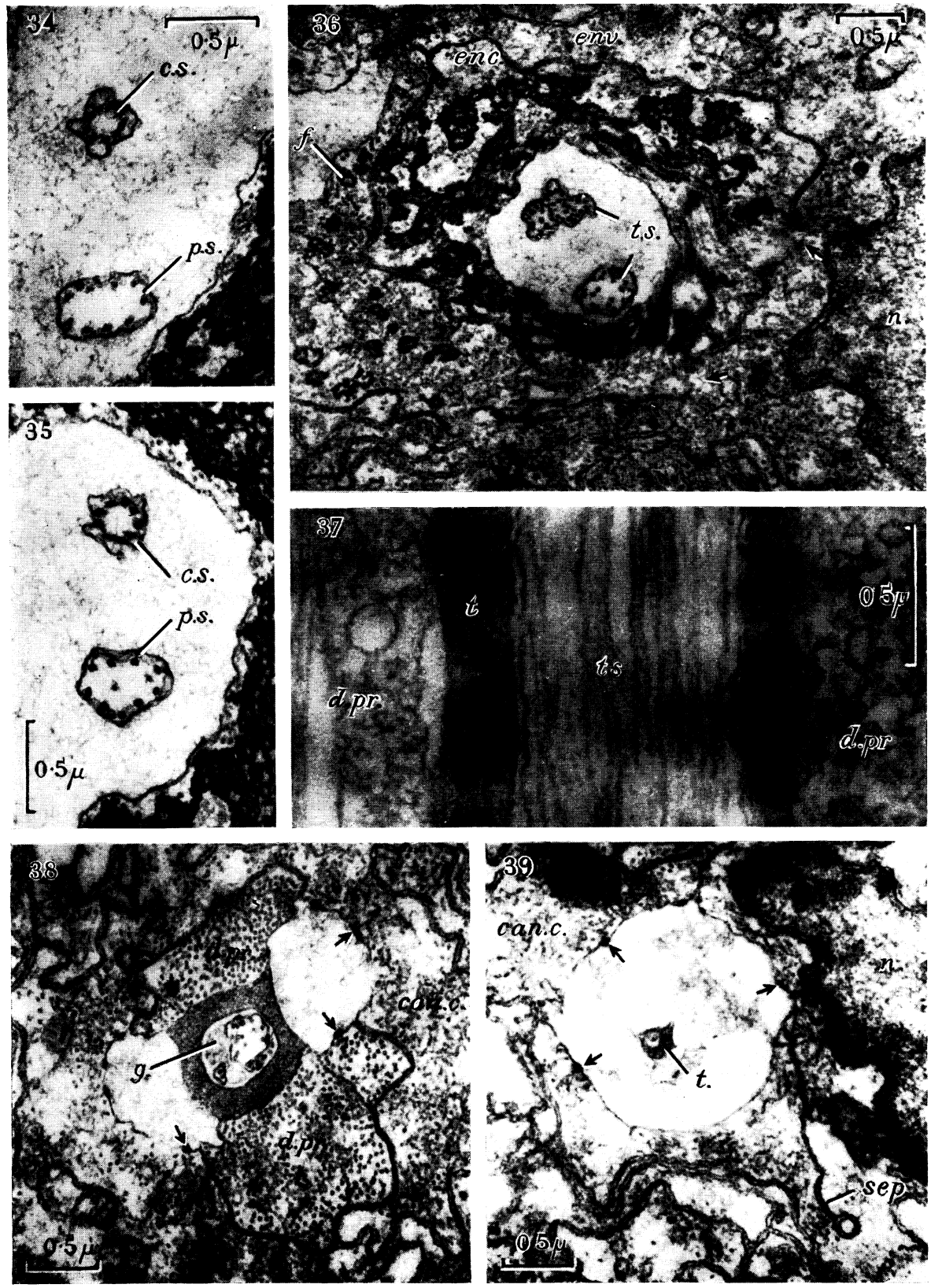
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37
t
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d.pr
38
con.c.
g.
d.pr
0·5μ
39
can.c.
n.
t.
sep.
0·5μ

Plate 60

Sections of *CP* 1, figure 37 longitudinal, the rest transverse.

Figure 34. Heterodynal scolopidium showing the ciliary segment, and the paraciliary segment without central filaments.

Figure 35. Similar to figure 34, but with the paraciliary segment with two central filaments.

Figure 36. Tip of scolopale with terminal segments. The nucleus is that of the scolopale cell. The arrows indicate gaps in the cell membranes between the scolopale cell enclave and its enveloping portion.

Figure 37. Longitudinal section of a tube with one terminal segment. The cell membrane of the distal prolongation of the scolopale cell is withdrawn from the tube at one place on the left.

Figure 38. Tube with two terminal segments, one of which is near its end and has only two tubules. There is 'glue' between the terminal segments. The distal prolongations of the scolopale cell are separated by canals, the whole surrounded by a canal cell. The arrows in this figure and in figure 39 indicate dark bodies on the cell membranes bounding extracellular spaces.

Figure 39. The extreme tip of a tube lying in an extracellular space bounded by the canal cell; the nucleus is that of the canal cell. An internal convolution of the canal cell membrane shows transverse septa.

Plate 61

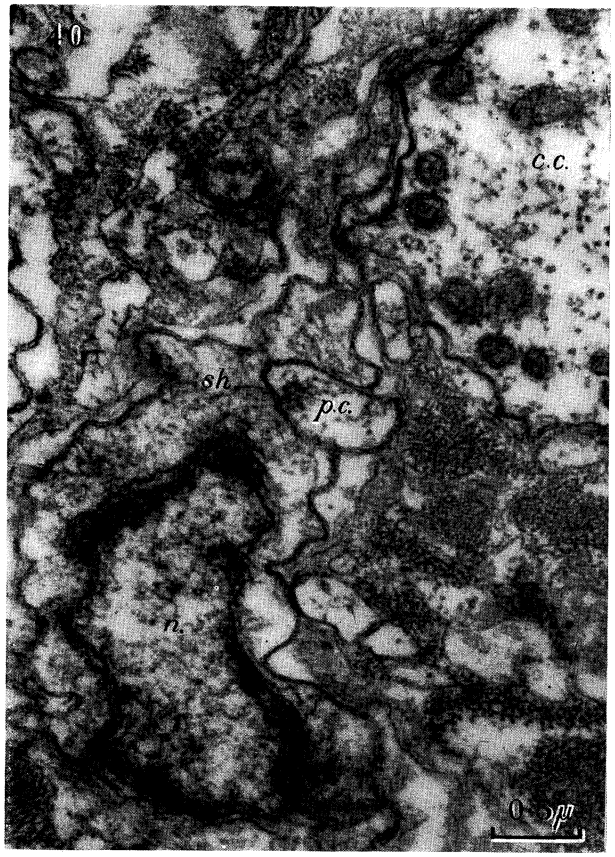
Transverse sections of *CP* 2.

Figure 40. Distal process of the paraciliary cell leaving its sheath cell as it approaches the distal process of the ciliary cell.

Figure 41. Distal process of paraciliary cell wrapped in the proximal extension of the scolopale cell enclave, which is separated from the distal process of the ciliary cell by part of the enveloping portion of the scolopale cell.

Figure 42. Section through the base of a scolopale showing attachment plaques between the distal process of the ciliary cell and the scolopale cell enclave. The distal process of the paraciliary cell is wrapped in the scolopale cell enclave and has only a fragment of axial filament.

Figure 43. Tube showing 'glue' and the tip of the terminal segment of the ciliary cell with only two tubules. One of the distal prolongations of the scolopale cell has some fibrous scolopale material.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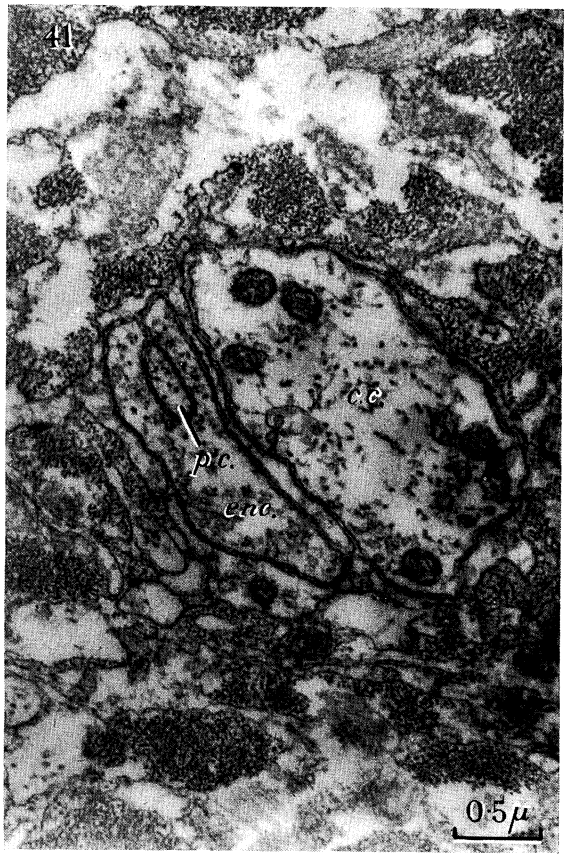
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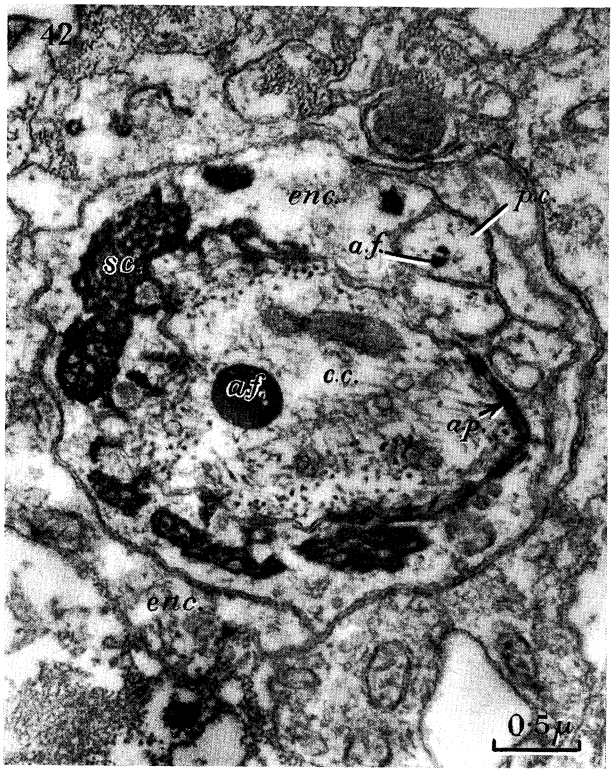
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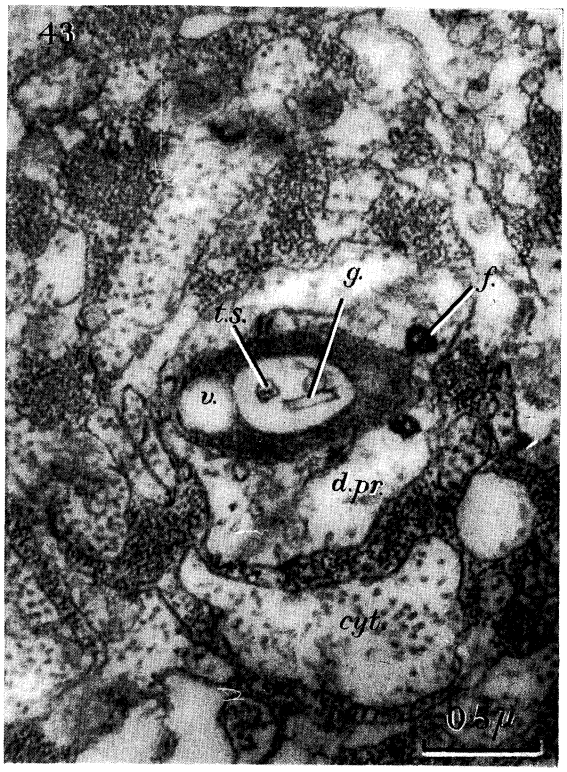
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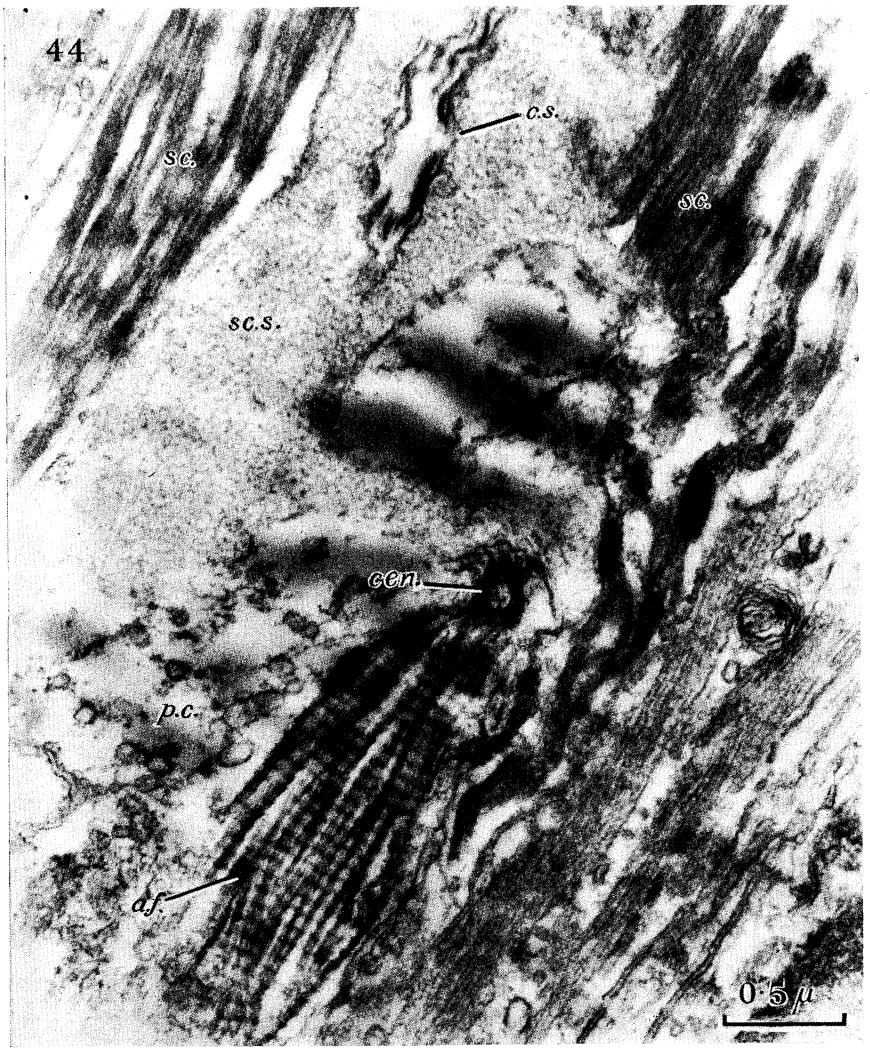
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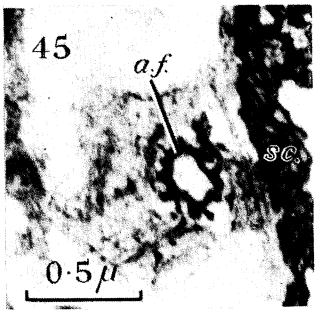
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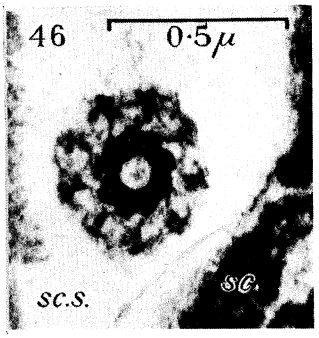
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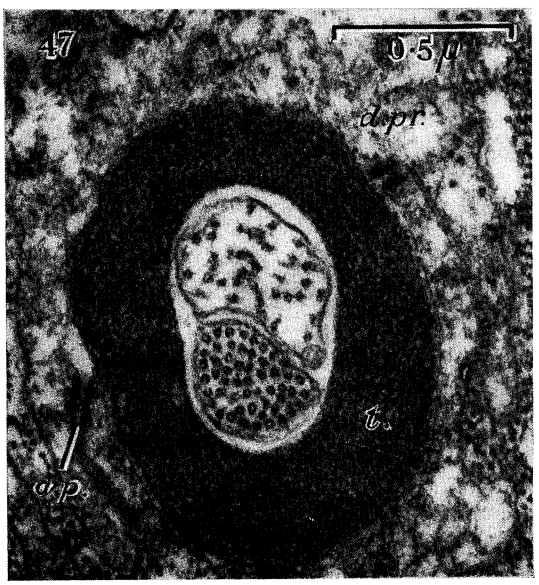
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t.
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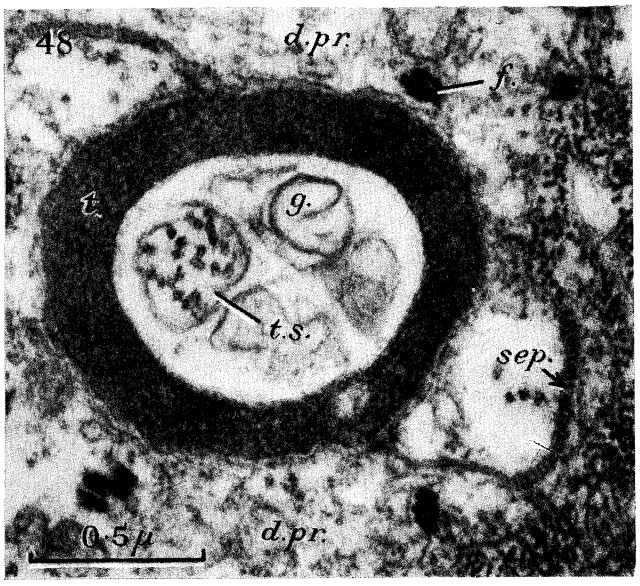
48
d.pr.
f.
t.
g.
t.s.
sep.
0·5 μ
d.pr.

shows the proximal end of a nucleus situated opposite the base of a scolopale; the enclave is on the other side of the distal processes.

Distal to the scolopale is the tube that corresponds to the 'terminal thread' of earlier descriptions of amphinematic scolopidia. The tube is an extracellular organ; in most micrographs a cell membrane can be seen outside it (figure 48, plate 62). Usually the walls of the tube appear granular and amorphous, rather like the amorphous connective tissue, but the tube material characteristically has rounded vacuoles at intervals. An extreme example is shown in figure 19, plate 57. Occasionally a lamellar appearance is seen at the base of the tube where it is overlapped by the tip of the scolopale. In a few cases, when tubes were near a part of the strand which had been damaged during preparation, the walls appeared distinctly laminated (figure 49, plate 62). The tube may have contents, of different kinds, mentioned later, but does not appear to contain the same substance as the scolopale space.

Distally the tube tapers until it ends as a solid strand. Some tubes are longer than others, but they never reach as far as the exoskeleton. Outside the tube, the cell membranes form two pairs of surface-connecting membranes, separating two regions of cytoplasm. It was previously thought (Whitear 1960*b*) that there were two cells responsible for secreting the tube, but it is now considered that a pair of *prolongations* arises distally from the scolopale cell, embracing the tube. When a good series of sections is available, it is not difficult to find the continuity between the enveloping portion of the scolopale cell and the prolongation on the side on which the scolopale cell nucleus lies, especially if the nucleus is in a distal position. The continuity of the cytoplasm of the opposite prolongation with that of the scolopale cell is more difficult to demonstrate, and it has not been possible to do this with confidence by the study of serial sections. In some cases, at least in *PD*, there is continuity of the two prolongations over the tip of the tube, but usually the two prolongations are distinct as far as they can be traced distally, even beyond the tip of the tube. Proximally, two pairs of surface-connecting membranes still occur in the enveloping region of the scolopale cell (instead of one as might be expected) as far as the level of the base of the scolopale; these can be found in figure 17, plate 57. The cytoplasmic connexion between the two pairs of prolongations must then be very indirect. Fortunately

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PLATE 62

Sections of *PD*, figure 44 longitudinal, the rest transverse.

FIGURE 44. A scolopale with part of the ciliary segment in the scolopale space, and the tip of the axial filament of the paraciliary cell with its centrosome. The cytoplasm of the paraciliary cell distal process shows numerous annular profiles.

FIGURE 45. Annular tip of the axial filament of a paraciliary sensory cell.

FIGURE 46. Distal process of a paraciliary cell showing the centrosome. The centriole is surrounded by nine peripheral masses.

FIGURE 47. Tube with the two terminal segments. There are attachment plaques on the surface-connecting membranes of the distal prolongations of the scolopale cell.

FIGURE 48. Tube with one terminal segment and 'glue'. There are transverse septa between the surface-connecting membranes of the distal prolongations of the scolopale cell.

FIGURE 49. Tube in a damaged specimen showing lamination of the walls.

there is another clue: in many specimens the cytoplasm of the scolopale cell contains fibrous material similar to that of the scolopale, but outside the scolopale enclave (this is why the definition of the scolopale was restricted to the material inside the enclave). This material does not seem to occur in any of the other cells associated with the scolopidia, but it is present equally in the cytoplasm on both sides of the tube, as in figure 29, plate 59.

The arrangement of the tissues surrounding the tubes differs in the different chordotonal organs. In *CB*, *MC*2 and *CP*2 the scolopale cell prolongations are surrounded by the collagen of the elastic strand, but in *MC*1, *CP*1 and *PD* another cell, the *canal cell*, intervenes. The cell outside the scolopale-cell prolongations may be the cap cell of light microscopists. The tube occupies a position similar to that of the 'cap' of locust ear scolopidia described by Gray (1960) but the appearance of its fine structure is not similar.

Summarising the information on the scolopale cell, it appears to consist of several distinct regions, connected by cytoplasmic bridges. These are: the scolopale enclave, the enveloping portion, and a pair of distal prolongations. Further, the enveloping portion itself is largely subdivided into two longitudinal halves, corresponding to the two distal prolongations, and also has numerous projections into the surrounding connective tissue.

Attachment plaques or desmosomes

Attachment plaques or desmosomes occur at certain places in the scolopidia. In this material no details of their structure can be made out; they appear as dark thickenings at opposite points on apposed cell membranes. There is no reason for supposing them essentially different from those described in vertebrate epithelia by Odland (1958), or Karrer (1960), or between Schwann cell membranes by Rosenbluth & Palay (1961). Gray (1960) found similar structures between the attachment cells in the locust ear, and possibly also between the distal process and the scolopale cell.

In the crab scolopidia attachment plaques are found on the cell membranes of the distal processes and scolopale enclave in the basal part of the scolopale (figure 33, plate 59), on the surface-connecting membranes of the scolopale enclave, on the surface-connecting membranes of the scolopale cell prolongations near the tube (figure 47, plate 62), and occasionally on cell membranes outside the scolopale cell, which probably belonged to projections from the enveloping portion.

There is a type of intercellular structure which in transverse sections appears as cross bars occupying the gap between two apposed cell membranes (figure 48, plate 62). These are apparently the same as those Wood (1959) described in *Hydra*, which he called 'septate desmosomes'. Wood shows them in longitudinal section as complete septa, but Gray (1960), who found similar appearances in insect material, interpreted his longitudinal sections as a 'honeycomb' of hexagonal compartments. In the present investigation a convenient 'frontal' section of the septa, between two cell surfaces, was seen only once (figure 15, plate 57). This slightly favours the interpretation of Wood that there are longitudinal septa, but the density of the septa is not constant along their length, so that the lines appear punctate.

In the crab chordotonal organs the septa have been seen in various places. For instance, they occur between the apposed membranes of sheath cells that form mesaxons, between axons and sheath cells, between distal processes of sensory cells and sheath cells, between

the distal processes of two sensory cells, between the scolopale cell and connective tissue cells, and between the various parts of the scolopale cell, that is, between the enclave and enveloping portion and between the various pairs of surface-connecting membranes. In short, the septa may occur wherever any cell membranes are in apposition. In some cases they must cover a considerable proportion of the surface in question.

Wood suggested that the septa were a form of desmosome or attachment plaque. As far as their appearance goes, the septa might as easily be keeping the cell membranes apart as holding them together. Wood's second suggestion that the septa form a diffusion barrier is also less apt here than in *Hydra*, especially as they frequently occur between the convolutions of the membrane of a single cell (figure 39, plate 60).

In addition to the attachment plaques and the septate desmosomes, dark bodies occur at intervals on the membranes of the outer parts of the scolopale cells. They look rather like attachment plaques, but are narrower and probably considerably elongated. In transverse sections they appear as dense thickenings of the cell membrane, with a separate dense spot in the cytoplasm next to it. Similar structures have been seen on sheath cells and probably on connective tissue cells, but are not so easily found there as on the scolopale cells. These dark bodies are not placed opposite another similar structure, but opposite a bundle of collagen fibres. Figure 17, plate 57, shows a number of these bodies on the enveloping portion of a scolopale cell, and figure 19, plate 57, shows them on the distal prolongations of a scolopale cell. Comparison of serial sections showed that similar appearances occurred in corresponding places in several sections some distance apart, so it seems likely that the structures have a considerable longitudinal extension, equivalent to the length of a scolopale in some cases. When, as sometimes happened, the collagen shrank away from the cell surface, it did so only between, and not opposite, the positions of the dark bodies. Such a condition is shown in figure 16, plate 57, from a section serial to that of figure 17; the equivalent dense bodies are indicated in the figures.

These structures are tentatively interpreted as modified attachment plaques, providing a firm union of the cells of the scolopidia with the connective tissue surrounding them.

Dark thickenings of the cell membrane were also seen sometimes next to an extracellular space, as in figure 38 and 39, plate 60.

Sensory nerve cells

All the nerve cells are bipolar primary sensory cells, with the diameters of the cell bodies ranging from 10 to 40μ in different parts of the organs. Two types of sensory cell can be distinguished, on the basis of the fine structure of their distal processes. In one type, the process as it crosses the scolopale space contains nine peripheral filaments, regularly arranged; this region is the *ciliary segment*. Near the tip of the scolopale the distal process thickens and the nine filaments diverge and change their structure; this region is the *paraciliary segment*. In the other type of sensory cell, the ciliary segment is absent, and the distal process as it crosses the scolopale space has the structure of the paraciliary segment of the first type of sensory cell. For convenience, the two types of sensory cell will be called ciliary and paraciliary cells respectively, though these terms are not entirely satisfactory, and would be better replaced by names expressive of the function of the cells, when those functions are understood.

Proximal to the scolopale, one description can apply to either type of sensory cell. The axons are wrapped in sheath cells, whether they are situated in the nerve or in the strand. Usually each axon has a separate sheath cell. The mesaxon may be partially spiral, or may be merely sinuous. Some axons share a common sheath (figure 14, plate 56). The diameter of an axon varies along the length of a fibre, if it is followed in serial sections. The axoplasm contains elongated mitochondria, and filaments of the 'thick' type, as described by Whitear (1960*a*) and by Elfvin (1961). These filaments are from 200 to 300 Å in diameter, and sometimes appear hollow. In longitudinal sections they show an irregular opacity, as described by Elfvin. A longitudinal section of an axon is shown in figure 30, plate 59.

The perikarya show some filaments, many mitochondria, endoplasmic reticulum, Golgi apparatus, in short the normal structure of nerve cells as described by Palay & Palade (1955). Cell bodies in the strand were particularly liable to show 'whorl-like structures'.

The distal processes of the sensory cells have more mitochondria than are found in the axons. These may be arranged near the periphery in the proximal part of the process, but elsewhere are scattered through the cytoplasm. 'Thick' filaments occur in the distal process as in the axon, but are less regularly arranged in the longitudinal direction. Numerous annular or irregular profiles are also seen, which are presumably parts of the endoplasmic reticulum (figure 31, plate 59).

Through most of their course in the strand the distal processes of a pair of sensory cells are separated by a narrow tongue of sheath cell, and within the base of the scolopale are similarly separated by an intrusive projection of the scolopale cell enclave, which in most cases contains some fibrous scolopale material. For a certain distance, however, sometimes within the scolopale but more often below it, at or even proximal to the level of the axial filaments, the two distal processes are in apposition, separated only by a 200 to 300 Å gap between the cell membranes (figures 31 and 32, plate 59). This condition has been seen invariably in all scolopidia sectioned at the appropriate level. It seems probable that there must be a functional significance in such a constant arrangement, and the region of apposition will therefore be referred to as the *ephapse*, a name invented by Arvanitaki (1942) to describe the locus of contact, or close vicinity, of two active functional surfaces, axon-axon or soma-soma. Whether or not there is a physiological interaction between the two sensory cells, at the ephapse, Arvanitaki's term is apt for the morphological arrangement. The number of mitochondria and annular profiles in the distal processes is the same in the region of the ephapse as elsewhere. There is no accumulation of vesicles. It is not possible to calculate the area of the ephapse exactly, nor is this constant, but it must usually be at least $5\mu^2$, and often larger; the scolopidia of *MC*2 and *CP*2 are exceptional, with a smaller ephapse. Axons may also be contiguous, and so may be the terminal segments, but these appositions are not called ephapses, because it is not a constant arrangement.

As it approaches the scolopale, each distal process contains an *axial filament*. This corresponds to the 'root' of Gray's description of the locust ear scolopidia (1960), but as it clearly corresponds also to the axial filament of previous accounts of scolopidia, as that of Debauche (1935), this term is preferred. The axial filament is commonly about $0{\cdot}5\mu$ in diameter, sometimes more, and tapers at the ends. Proximally it ends in a point, not in

'rootlets' as in the locust ear sensory cells. In transverse sections the axial filament appears dark, with occasional holes in the substance (figure 20, plate 57). In longitudinal sections it is seen to be cross-striated in a complex fashion (figure 44, plate 62). The major period of the striations is usually about 700 Å. The striations evidently correspond to those of Gray's root, but are not seen in such detail. There are, proximal to distal: a thick dense line which projects a little at the sides, a pale line of about the same thickness, a thin dark line, usually indistinct, and a grey line. Sometimes all the lines except the palest merge as a broad dark band, so that the polarization of the filament cannot be seen. Occasionally an axial filament was found to be much bent, even though neighbouring axial filaments were straight. The form of the distal end of the axial filament differs in ciliary and paraciliary sensory cells.

About half way along the length of the scolopale, the two distal processes narrow. Mitochondria occur in the distal processes up to this point, but not beyond it. There are fewer filaments, and an abundance of annular profiles, in the cytoplasm just proximal to the point of narrowing (figure 44).

In the basal half of the scolopale, attachment plaques are found on the cell membranes of the distal processes and of the scolopale cell enclave (figure 33, plate 59). They look similar in transverse and in longitudinal sections. Sometimes the plaque on the scolopale cell wall has a projection of the scolopale reaching to it, but other projections of the scolopale to the cell membrane occur elsewhere where there are no attachment plaques, particularly towards the tip of the scolopale (figure 26, plate 58).

Near the point of narrowing of the distal process, and immediately beyond the tip of the axial filament, lies a centrosome, which resembles those described by Bernhard & de Harven, (1958), or the basal bodies of flagellates described by Gibbons & Grimstone (1960). A centrosome appears in longitudinal section in figure 44, and in transverse section in figure 46, plate 62. The centrosome may be in a part of the distal process in the lumen of the scolopale, or may be where the distal process lies against the scolopale wall. The centrosome of figure 46 belonged to a paraciliary cell which was anomalous in that the more distal parts of the sensory cell were missing; it happened to be a particularly clear picture of the nine peripheral masses around the centriole, but these structures have been seen in normal sensory cells as well. No difference was detected between the centrosomes in the ciliary and paraciliary types of sensory cell, though the structures both proximal and distal to them do differ. Bodies that appear to be the centrosomes of a sheath cell and of a scolopale cell respectively occur in figure 22 and 23, plate 58; in both cases they were near, and distal to, the nucleus.

It is necessary to describe the remaining structures in the two varieties of sensory cell separately. In the ciliary type, the distal end of the axial filament tapers and is flattened at the tip. The distal process narrows, leaves the scolopale wall, and crosses the scolopale space to enter the tube. Distal to the centrosome the process acquires the fine structure of a sensory cilium, with nine peripheral double filaments. This part of the sensory cell is the ciliary segment. Each of the nine peripheral filaments appears to consist of a rod and a tube, like those of the cilium of locust ear sensory cells (Gray 1960). There is a pair of projections (arms) from the side of the rod (figure 25, plate 58). In motile cilia each of the nine peripheral filaments consists of a pair of tubules, but Gibbons (1961) mentions that the

subfibre bearing the arms may have a dense core, due to a backward extension of one of the arms.

At the base of the ciliary segment the filaments appear to arise from a ring which follows immediately on the centriole (figure 21, plate 57). The nine peripheral filaments bear a constant relationship to each other in that they always lie at regular intervals as if on the circumference of a cylinder of diameter about 0·15 μ. This is similar to the arrangement of the peripheral filaments in motile cilia, but no central structures were seen in the ciliary segment of a sensory cell. The cell membrane of a ciliary segment usually appears irregular. Part of a ciliary segment is cut longitudinally in figure 44, plate 62.

It is necessary to restrict the definition of the ciliary segment to that part of the distal process having nine double peripheral filaments on the circumference of a cylinder 0·15 μ in diameter, because the filaments continue distally into another region with a distinct structure. This is here called the paraciliary segment. Beyond the ciliary segment, while still within the scolopale space, the distal process broadens somewhat, and the nine peripheral filaments diverge so that in transverse sections they lie on the circumference of a circle of diameter about 0·3 μ. As they diverge they lose their former constant relationship to one another, and appear to consist of two tubules instead of a tubule and a rod; the arms disappear. These changes can be compared with those described by Gibbons (1961) near the tip of a motile cilium. In the proximal part of the paraciliary segment the centre of the distal process still looks empty, but shortly a few central filaments appear. There may be from one to five central filaments, which usually look solid and ill-defined. In figure 26, plate 58, one of the central filaments is present; four more appeared in serial sections intermediate between figures 26 and 27, which is at a level intermediate between the paraciliary segment and the next segment of the distal process. Sometimes there seem to be connexions between the central filaments of the paraciliary segment (figure 18, plate 57), but this appearance might be due to the filaments interweaving and crossing close by each other. The paraciliary segment must not be confused with the 'ciliary dilatation' of Gray (1960) which is a different structure with no counterpart in the crab sensory cells.

As the distal process of the sensory cell leaves the scolopale space and enters the tube the paraciliary segment merges into the *terminal segment*, characterized by the presence of numerous tubules about 200 Å in diameter. These are single tubules (figure 47, plate 62) but may have a projection at one side, which sometimes links adjacent tubules. In some specimens, probably overstained with *PTA*, there were dense black areas between some of the tubules. In longitudinal sections (figure 37, plate 60), the density of the tubules does not appear quite constant along their lengths, but they are more distinctly tubular than the thick filaments of the axons. The nine double filaments of the paraciliary segment can be traced for some distance on the periphery of the proximal part of the terminal segment (figure 27, plate 58), but then disappear. The terminal segment may be considerably thicker than the paraciliary segment; it tapers before it ends distally.

In the paraciliary type of sensory cell the tip of the axial filament is complex in form. In transverse sections, followed proximally to distally, first the outline of the axial filament becomes crenellated, then much incised; a hollow appears in the middle, and the extreme tip shows an annulus with external rays. Though the annular tip is always found, its

size varies in different scolopidia. Beyond the tip of the axial filament is the centrosome, then a ring like that at the base of the ciliary segment, only, as it was rarely seen, it is probably not prolonged as far distally as in the ciliary cell. The incised part of the axial filament is seen in figure 33, plate 59 (there are two small subsidiary axial filaments in this section) and the annular tip in figure 45, plate 62. Figure 21, plate 57 shows the extreme tip of the centriole.

In the paraciliary cell there is no ciliary segment. Instead, a paraciliary segment, with nine double hollow filaments on the periphery, follows on the ring. As in the ciliary cell, the centre of the paraciliary segment is empty proximally (figure 34, plate 60) but more distally a few central filaments appear. There are two in figure 35. The length of the paraciliary segment of the paraciliary cells varies in different scolopidia, and is usually longer than is the paraciliary segment in ciliary cells. It merges distally into a terminal segment, which has essentially the same structure as in the ciliary cell, though the two terminal segments are often of unequal size, and one may be more densely packed with tubules than the other (figure 47, plate 62). Variations in the form of paraciliary cells are described in a later section.

The two terminal segments usually occupy most of the lumen of the tube of the scolopidium, in its proximal part. Their extent in the tube varies greatly, but they never reach throughout its whole length. They may be about the same length, or one may extend some way beyond the other. They taper at the ends, and the number of tubules becomes reduced (figure 38, plate 60). Around the tips of the terminal segments is found an indistinct appearance as of tangled membranes (figure 38, plate 60). Previously (Whitear 1960*b*) this was referred to as 'glue', and no better name can at present be found for it. As it is only found around and just beyond the tips of the terminal segments, and as occasionally it appears to connect them to the wall of the tube, it is thought that the function of this substance may be to fasten the terminal segments into the tube, a suggestion which is of course entirely speculative. Beyond the ends of the distal processes the tube usually appears empty, but on a few occasions a lump of granular material appearing quite different to the 'glue' has been found well beyond the distal processes (figure 28, plate 58).

Numbers of axons

A chordotonal organ can be prepared in such a way that the accompanying tendon nerve is removed, and the nerve from the scolopidia sectioned and viewed in the electron microscope. It might be expected that this procedure would give an accurate figure for the total number of axons leaving a chordotonal organ, but, though the larger axons can be counted, there is difficulty in distinguishing small axons from lobules of sheath cells.

Figure 14, plate 56, shows part of the nerve from *CB*, with two bundles of what appear to be small axons wrapped in a single sheath cell. If these are all separate axons, there are twelve in one bundle and twenty-eight in the other. The appearance is like that of the developing unmyelinated nerve fibres described by Peters & Muir (1959) in foetal rats before the Schwann cell cytoplasm has appeared between individual fibres. Comparable appearances, though less tidy, were found in other nerve bundles. It is difficult to identify individual fibres in serial sections as they interlace and may pass to different sheath cells. In another *CB* nerve there were two bundles of what appeared to be small axons. If all the

apparent small 'axons' in this nerve were counted as such, the total number of nerve fibres leaving the chordotonal organ was 224, but if the two anomalous bundles were excluded, it was 102. Some of the small 'axons' may have been lobules of sheath cells. The minimum figure for the number of axons leaving *CB* may be taken as about 100, which fits well enough with the numbers observed in methylene-blue preparations. The appearance of the nerves in methylene-blue preparations would not lead one to suppose that there is any fusion of axons.

Variations in the structure of the scolopidia in different chordotonal organs

All the scolopidia of the crab leg chordotonal organs have paired sensory cells. In *CB* the two cells are similar, both being of the ciliary type. These scolopidia can be called *isodynal*. In the more distal chordotonal organs the two sensory cells are dissimilar, one being of the ciliary and one of the paraciliary type. These can be called *heterodynal*. Three varieties of heterodynal scolopidia have been found, which are illustrated in figure 11, p. 304; the relative development (or complication) of the two cells varies. In the figure, the proportions of the scolopale are approximately correct, but the parts more distal and more proximal have been shortened, for convenience. The descriptions apply mainly to the scolopidia in the proximal parts of the strands, as these are usually the largest, but any differences in the more distal scolopidia are trivial.

PD *organ*

The scolopidia of *PD* are of the heterodynal type illustrated in figure 11*A*. The distal processes of the ciliary and of the paraciliary sensory cells are of approximately the same size. The attached part of the paraciliary cell distal process extends further into the scolopale than does that of the ciliary cell, and usually also has the axial filament more prolonged proximally. The two axial filaments are of about the same thickness at their greatest diameters. A ridge of the scolopale wraps the distal process of the paraciliary cell.

The proportions of the more distal parts of the sensory cell processes were not the same even in neighbouring scolopidia of a single specimen. Some scolopidia showed the paraciliary segment of the ciliary cell opposite the terminal segment of the paraciliary cell, as in figure 11*A*, but in others it was the other way round. It was common to find the terminal segment of the ciliary cell more packed with 200 Å tubules than was that of the paraciliary cell, but this was not invariably so. Either terminal segment might be the thicker. Occasionally the terminal segment of the paraciliary cell was grossly swollen in the scolopale space (this was seen also in other organs).

It was common for the prolongations of the scolopale cell on either side of the tube to contain small bundles of scolopale material. One of the two pairs of surface-connecting membranes between the two prolongations disappeared near the the tip of the tube so that there was cytoplasmic continuity between the two prolongations. In some scolopidia the distal half of the tube was flanked by two canals formed by the drawing apart of the surface-connecting membranes. The outer sides of these canals were bordered by the canal cell, which enwrapped the scolopale cell prolongations on the outside.

CP2 *and* MC2 *organs*

In the preliminary report of this work (Whitear 1960*b*) it was stated that the 2 scolopidia had only one sensory cell; this was an error. A second, paraciliary, cell is present, but for several reasons is inconspicuous. The scolopidia of *MC*2 resemble those of *CP*2. Figure 11*B* represents the typical form of these scolopidia. The ciliary cell is normally developed. The paraciliary cell distal process is slender, often less than half a micron in diameter, and its terminal segment is short and small, with few tubules. In some scolopidia the paraciliary and terminal segments of the paraciliary cell are better developed than in figure 11*B*. In that figure the sheath cell nucleus is drawn, because in a number of scolopidia of these organs it was more distal in position than was usual in the other chordotonal organs. It appeared not far proximal to the scolopale cell nucleus (sometimes they overlapped) and at a level at which the paraciliary cell process was wrapped in the scolopale cell enclave. Occasionally in the other organs as well the sheath cell nucleus was not far from the scolopale cell nucleus.

The distal processes of a pair of cells do not approach each other until relatively near the scolopale. Figure 40, plate 61, shows the small distal process of the paraciliary cell leaving its own sheath cell as it approaches the larger distal process of the ciliary cell. On reaching the immediate neighbourhood of the ciliary cell, the paraciliary cell process becomes wrapped in a special proximal prolongation of the scolopale cell enclave (figure 41).

The base of the scolopale is unevenly developed, and may form a single stout wall rather than a cylinder (figure 23, plate 58). There is an ephapse, either within or below the scolopale, but the area of apposition is small (figure 22). The distal process of the paraciliary cell, though within the scolopale cell enclave, may be outside the wall of the scolopale itself. It does not reach so far into the scolopale as does the ciliary cell process before passing into the scolopale space. The centrosome of the paraciliary cell is normally developed, but the axial filament consists only of an irregular annulus (figure 23) with a few small proximal projections (figure 42, plate 61). Few mitochondria are found at this level, or indeed anywhere in the distal process; sometimes there is a single large one near the axial filament.

In the scolopale space, the paraciliary segment of the paraciliary cell is followed by a small terminal segment with few tubules, which reaches only a short distance into the tube. The distal prolongations of the scolopale cell are in direct contact with the connective tissue of the strand, not wrapped in another cell. There might be a few fragments of scolopale material in the prolongations (figure 43). Canals by the tube were not seen, though in one case there was a space by the tube tip.

In some specimens, the two sensory cell processes were more evenly developed in the most distal scolopidia of the strand. In no case was it possible to trace the positions of the cell bodies of both the cells of a pair, so that it is not known if they also differ in size. In a nerve which was examined, there was no sharp division of the axons into two sizes.

There were two reasons for missing the paraciliary cells in the early series of sections: first, the small size of the distal process, and secondly, the accident that in the scolopale space the process was often broken (apparently after fixation) so that there appeared to be only the ciliary process. It is presumed that the breaks occurred when the chordotonal

organ was stretched, after the initial fixation, by fixative reaching the muscles. Breaks were seen occasionally in other organs also, but never affected the ciliary cell process, except in one doubtful case. Figure 24, plate 58, shows an example of a break in the terminal segment of a paraciliary cell; the tubules of the terminal segment can be seen loose in the scolopale space, and the cell membrane coiled up in a spiral. In figure 26, which is from the same series not far away, the terminal segment of the paraciliary cell is intact again. Often the breaks were more extensive and the debris lost among the wisps of material normally occupying the scolopale space. Even if the terminal parts of the paraciliary cell were not damaged, they might be inconspicuous, especially if the terminal segment had few or no tubules and lay close against the wall of the scolopale; then it could be mistaken for a small projection of the scolopale cell enclave. Such projections were quite common (one occurs in figure 24) and the cytoplasm often contained a few tubules. Sections of the tube, unless very near its base, showed only one terminal segment. More proximally, the paraciliary cell distal process when first seen was interpreted as part of the scolopale cell enclave, for in transverse sections the scraps of axial filament look very like scolopale material, as in figure 42, plate 61. More proximally still, the distal process is so small it may be difficult to find in some sections.

CP1 *and* MC1 *organs*

In these chordotonal organs, in contrast to the preceding ones, the paraciliary sensory cell is particularly well developed. The condition is illustrated in figure 11*C*. The ciliary cell is normal in appearance. The paraciliary cell has an axial filament both longer and thicker than that of the ciliary cell, though in spite of this its distal process is usually the smaller in diameter (figure 20, plate 57). The tip of the axial filament of the paraciliary cell is much cut up, and there may be small subsidiary axial filaments (figure 33, plate 59).

The attached part of the ciliary cell distal process usually extends slightly further into the scolopale than that of the paraciliary cell, but there is not much difference between the two cells in this respect, and in one series of proximal scolopidia from an *MC*1 organ it was the other way round.

The paraciliary segment of the paraciliary cell is often longer than in the scolopidia of the other chordotonal organs. The terminal segments are more or less equal in thickness. One may have more tubules than the other, and sometimes the tip of one is divided into several small processes.

Fibres of scolopale material are found not only in the distal prolongations of the scolopale cell (figure 29, plate 59) but also in the enveloping portion (figure 36, plate 60). Well-developed canals are present on either side of the distal half of the tube (figure 38) which are continuous distally with a space in which the extreme tip of the tube lies free (figure 39). This space is enclosed by the canal cell which more proximally wraps the distal prolongations of the scolopale cell. Usually there is one canal cell to each scolopidium, but there may be more, and two adjacent tubes may share three canal cells. The distal prolongations of the scolopale cell become narrower as they pass distally, and the canals wider. Sometimes the extreme tip of the tube (which in figure 39 is beyond the ends of the distal prolongations) lies against the wall of the extracellular space. It cannot be asserted that the canals are invariably present, as not all the tubes were followed distally, but they

are characteristic at least of the proximal scolopidia of *CP*1, and do occur in some cases distally. It so happened that the distal parts of the tubes were not followed in the *MC*1 specimens.

Occasionally the two axial filaments are of approximately the same size, so that the scolopidia resemble those of *PD* except that the paraciliary cell process does not reach so far into the scolopale. A number of anomalous scolopidia were seen: in a few cases from *CP*1 and from *MC*1 only one axial filament was present, which might be that of either cell. Two of these anomalous scolopidia were of the proximal and lateral group of *MC*1; they were close together, and had the paraciliary cell distal process of normal size but without an axial filament. It was not often possible to be confident whether particular proximal scolopidia were lateral or mesial in *MC*1. In a number of scolopidia of these organs the terminal segment of the paraciliary cell was grossly swollen.

CB *organ*

The scolopidia are isodynal, with two similar sensory cells of the ciliary type, which are the same in structure and proportions as the ciliary cells of the other chordotonal organs. One distal process of a pair may be larger than the other, and sometimes the cytoplasm looks dissimilar in the two distal processes, but these are minor differences. Similarly, the two terminal segments may not be of the same thickness. The transitions from ciliary to paraciliary to terminal segments usually take place at the same level in both cells, and the axial filaments are of approximately the same length. Figure 18 shows the two paraciliary segments, which are short, side by side.

Discussion

Burke (1954) found that the *PD* organ could signal the rate and extent of movement at the joint, and thought it might also be used as a vibration receptor. Wiersma & Boettiger (1959) confirmed Burke's results on *PD* but did not agree that the organ would normally be used to detect vibrations. In addition, they showed that individual sensory cells responded to movement in one direction only. Certain fibres discharged only during movement. Other fibres showed little response to movement but increased the frequency of discharge in response either to greater degrees of flexion, or to greater degrees of extension, of the joint. Wiersma & Boettiger speak of these fibres as coming from 'movement' cells and 'position' cells respectively, though the distinction was not clear-cut and some cells could not be put in either category.

These authors distinguish, then, four types of sensory cells: (1) flexor movement cells, (2) extensor movement cells, (3) flexor position cells and (4) extensor position cells. Their results also indicated that in *PD* the movement receptor cells were large and situated proximally in the organ, while the position receptor cells were small and situated distally, that is, embedded in the strand. Further, they suggested that the extensor movement cells of *PD* were those situated dorsally and loosely attached to the strand, while the flexor movement cells were more ventral (on the tendon side) and more closely associated with the strand. Wiersma (1959) made recordings from the *PD*, *CP* and *MC* chordotonal organs of several species of decapods, and found in all organs the four types of response described above.

Unidirectional responses

The sensory cells are differentiated into two types, the 'ciliary' and 'paraciliary'. The most obvious hypothesis about their functions is that one cell is the flexor and one the extensor receptor. As they are situated closely side by side in the strand, both nerve endings must suffer equal stretch when the organ is extended; therefore it is assumed that one cell will fire when the tension on it is increased, and the other when the tension is relaxed. Unfortunately the scolopidia are too small and too inaccessible to be observed directly in a fresh condition; one can only guess at the relative movements undergone during stimulation.

J. A. B. Gray (1959) suggests that functionally mechanoreceptors can be divided into three parts: (1) a mechanical system that transmits and modifies the mechanical energy, (2) the biological transducer in which the electrical energy is developed, and (3) an electrical system that transmits the output of the transducer to the site of impulse initiation. It may be profitable to look for histologically distinct regions in the scolopidia which correspond to these three parts.

The scolopale and the tube must certainly be part of the mechanical transmitting system. It seems reasonable to regard the tube as the part that is stretched, and the scolopale as a rigid point of reference. The presence of attachment plaques between the distal processes of the sensory cells and the walls of the scolopale cell enclave, in the basal half of the scolopale, is suggestive, as attachment plaques do not occur elsewhere on the distal processes.

If the scolopale is a relatively rigid organ, and if the distal processes of the sensory cells are fixed by attachment plaques at a particular distance within the scolopale, there will be a fixed distance between the tip of the axial filament and the tip of the scolopale. If the ends of the terminal segments are fastened into the tube by the 'glue', any stretch of the tube will be transmitted to the terminal segments at the point of attachment, and will alter either the curvature of or the tension on those parts of the distal processes that lie across the scolopale space.

In the ciliary type of cell, it is evident that the curvature of the ciliary segment is not the same in all the scolopidia examined. In figure 11 the ciliary segments are drawn in what is conceived to be the extended position, with little curvature; this was the common condition in the material, when the ciliary segment would be cut in approximately transverse section even towards the base. In some scolopidia, however, the base of the ciliary segment was cut in oblique section, indicating that the process curved strongly as it left the wall of the scolopale space. The example shown (figure 16, plate 57) is from *CB*, but can be matched from other organs. As the curvature of the ciliary segment does demonstrably vary, it will be supposed that a change in the curvature of this part of the sensory process is the adequate stimulus for firing of the ciliary sensory cell.

The distal process of the paraciliary cell has not been seen to have a pronounced curvature on leaving the wall of the scolopale. Further, it was this distal process, not the ciliary one, which occasionally broke during preparation. Possibly, then, the mechanical properties of the two sensory cell processes differ, and the adequate stimulus for the firing of the paraciliary cell might be a change in tension of the paraciliary segment rather

than a change in its curvature. It must be admitted that the positive evidence with regard to the behaviour of the paraciliary cell is slight.

Reverting to the three parts of an ideal mechanoreceptor, the scolopale, tube and 'glue' would form the mechanical system, while the transducer would be associated with the terminal segment, paraciliary segment and ciliary segment when present. All parts proximal to the centrosome would form part of the conducting system to the axon.

Comparing the structure of the scolopidia of the various organs of the leg with their functions as reported by Wiersma (1959), it does appear that the simple hypothesis that one cell of a pair responds to stretching and one to relaxation of the strand (and therefore of the distal parts of the sensory cells) is tenable as far as the *PD*, *CP* and *MC* organs are concerned. The interesting organ is *CP*2, which responds predominantly to movement in one direction only, whereas in the other organs two sets of unidirectional fibres are found. The fact that the distal processes of the paraciliary cells are so poorly developed in *CP*2 suggests that Wiersma was recording only from ciliary type sensory cells. Four out of the five *CP*2 organs investigated by Wiersma responded mainly to flexion (production), during which movement the elastic strand is shortened. It follows then that the ciliary cell most probably fires during shortening of the strand, when the curvature on the ciliary segment is supposed to be increased.

Wiersma found that the *CP*1 organ responded to movements in both directions, with some tendency for the extensor response to dominate. As *CP*1 is stretched during the contraction of the muscle on its own side, and relaxed during reduction (extension) this suggests that he was again recording mainly from ciliary sensory cells. The paraciliary cells are, however, at their greatest relative development in *CP*1.

In *PD*, the idea that one cell responds to stretch and the other to relaxation fits very well with the results of Wiersma & Boettiger (1959). About half the fibres respond to extension of the dactylopodite and half to its flexion. As the two cells of a pair are here about equally developed, it might be expected that the chances of recording from their fibres would be about equal.

The hypothesis suggested, that unidirectional reception depends on a structural differentiation of the sensory cells into two types, could be tested by experiments on the *CB* organ, which contains only ciliary type sensory cells. If *CB* responds to movement of the joint in *both* directions, the hypothesis fails at once. If *CB* responds to movement in one direction only, the hypothesis is tenable, and there will be a check on the function of the ciliary cells. The *CB* elastic strand is stretched during depression of the leg, and shortens during its elevation. From the results on *CP*2, it would be expected that *CB* would fire when the levator muscles contract.*

Even if the sensory cell differentiation hypothesis is not contradicted by experimental evidence from *CB*, it is not, in the simplest form, entirely satisfactory. It would not explain why two cells are always present even in *CB* (where they are identical) and in *CP*2

* While this paper was in the press, Dr Bush kindly communicated to me the preliminary results of his investigation of the *CB* organ. He finds unidirectional movement fibres for both directions, and also position fibres for both directions. *CB* therefore appears to show the same range of responses as *PD*, in spite of the fact that the scolopidia of one are isodynal and of the other, heterodynal. The hypothesis suggested above will not now explain all the facts, and the functional meaning of the observed differences in structure of the two types of sensory cells remains obscure.

(where one of them may have a very slender distal process). The pairing of the sensory cells does suggest, as does the invariable presence of an ephapse, that interaction between the two cells may be involved in their functioning. Further, it is the paraciliary cells which show variation in development; the ciliary cells, with very few exceptions, have a remarkably constant structure. The major difference between the two cells is in a sense a negative one. The supposed transducer region of the paraciliary cell consists of the paraciliary and terminal segments; regions histologically indistinguishable from these occur distal to the ciliary segment in the other cell type.

'Position' and 'movement' receptors

Wiersma & Boettiger (1959) classify the proximal sensory cells of *PD* as 'movement' receptors, and the distal cells as 'position' receptors. Wiersma (1959) also found movement and position fibres in the *CP* and *MC* organs, without tracing these fibres to particular groups of cells. In all the organs the proximal sensory cells are usually larger than the distal ones. The size of the scolopales also tends to be less in the more distal scolopidia, though this size difference is not so pronounced as is that of the sensory cell bodies.

If there is a morphological difference between scolopidia acting as 'movement' receptors and scolopidia acting as 'position' receptors it must be a subtle one, for in this investigation no constant differences, other than of size, have been detected between the scolopidia of proximal and distal sensory cells. In one case, the most distal scolopidium of a *CP*2 organ was found. It was small, with the axial filaments scarcely developed, but ciliary and paraciliary processes were present. This scolopidium and two others near it had the two distal processes more or less equally developed, but, in other specimens of *CP*2, scolopidia which were classified as distal had unequal distal processes.

Some differentiation of threshold might be based on the properties of the tissues surrounding the scolopidia. Some parts of the strand may have less resistance to stretch than others. Movement of the joint would then stretch the weaker part of the strand more than the stronger part, so that the tubes in the one would undergo a particular threshold tension earlier than those in the other. The scolopales are scattered in the strand in such a way that two rarely occur at exactly the same level, even when, as sometimes happens, they occur in pairs. In *CP*1 and *MC*1 both the attachments of the strand and the arrangement of the scolopidia are complex, but constant. It is difficult to see, however, how this sort of differentiation could account for the observed distinction that the position cells are more distal than the movement cells.

Isodynal scolopidia

The function of the *CB* organ remains to be discovered. If it should, as seems likely from the available histological evidence, register elevation of the leg, this may have importance in the autotomy reflex. It is true that the levator muscle has another proprioceptor associated with it, the levator innervated elastic strand, but this is more likely to be concerned with the movements of the leg as a whole during walking (see discussion in Alexandrowicz 1958). According to Wood & Wood (1932) autotomy occurs when the musculus levator basipoditis contracts to such an extent that the basipodite is pulled under the rim of the coxa, and the leverage so exerted distal to the fracture plane breaks the leg.

In such a position of the limb, *CB* would be at its minimum length. *CB* is ideally situated to measure the angle between the coxa and the basi-ischiopodite. It seems probable that its function may be to provide information about the angle of this joint so that the levator muscle does not contract beyond a safe point, save when afferent impulses from the limb initiate the autotomy reflex and override the information from *CB*. The absence of paraciliary sensory cells would be explained by the fact that the organ was only concerned with decrease in the angle of the joint, or the measurement of angles near the elevated position of the leg.

Comparison with sensory nerve cells described from other sources

The number of detailed studies of the fine structure of sensory cells is too limited to attempt to make deductions about function from comparison of different endings. Nevertheless, it is worth while to review briefly those sensory endings described which appear comparable with those of the crab leg chordotonal organs.

The only other scolopidia investigated by electron microscopy are those of the locust tympanal organ described by Gray (1960). An obvious difference is the pairing of the sensory cells in the crab but not in the locust. The substance of the axial filament appears to be similar, but the form of both ends of the axial filaments differs in the two animals. Gray did not describe a centrosome, but comparison of his figure 29 with figure 44, plate 62, here suggests that the structure he labels 'base of cilium' in that figure (not in others) may be a centrosome. The fine structure of the ciliary filaments appears the same in both sites, but there is no counterpart in the crab of Gray's 'ciliary dilatation', nor in the locust of the paraciliary and terminal segments. The end of the distal process in the locust, distal to the ciliary dilatation, regains a ciliary structure, and it is this part which inserts into the 'cap'. Though the cap corresponds in position to the tube, their fine structure is not the same. The form of the scolopale in the locust ear is more regular and more constant than in the crab chordotonal organs.

The only other insect sensory cells so far described which have a fine structure comparable to those of the crab chordotonal organs are those of the plate organ of the antenna of a honey bee (Slifer & Sekhon 1960, 1961). The authors say that the distal processes of these cells have the fine structure of typical cilia. Examination of their figures suggests, however, that this fine structure has actually more resemblance to the paraciliary segment of crab sensory cells than to the ciliary segment. Central filaments are sometimes present and the nine peripheral filaments have the spacing of those in a paraciliary segment. There is a centrosome which appears to be similar to that described above in crab sensory cells.

References to descriptions of other sensory cilia will be found in Fauré-Fremiet (1961). Salpeter & Walcott (1960) have described the fine structure of the sensory cells of the lyriform organ of a spider. There is little in these cells to compare with the crab sensory cells, unless the tubules which were sometimes seen in the distal part of the sensory cell correspond to those in the terminal segment. Nor are the sensory cells of the cerebral vesicle of ascidian tadpoles (Dilly 1961) like the chordotonal organ ones, except that there also attachment plaques occur proximal to what may be presumed to be the transducer of the sensory cell.

Appendix

Number of specimens used in the investigation:

organ	total number of animals	total number of specimens	number of specimens yielding useful series
CB	3	3	3
*MC*1	2	2	2
*MC*2	2	6	1
*CP*1	2	3	3
*CP*2	4	7	6
PD	3	7	5

A specimen might be useless either because it was badly fixed or badly embedded, or because the sections taken failed to show any scolopales.

Key to the abbreviations used in the plates and in figure 11

a.c.t.	amorphous connective tissue	*f.*	fibrous scolopale material
a.f.	axial filament	*g.*	'glue'
a.p.	attachment plaque	*l.*	lumen of tube
ax.	axon	*m.*	mitochondrion
c.	collagen fibres	*n.*	nucleus
c.c.	ciliary sensory cell	*p.c.*	paraciliary sensory cell
c.s.	ciliary segment	*p.s.*	paraciliary segment
can.c.	canal cell	*s.c.m.*	surface-connecting membranes
cen.	centrosome	*sc.*	scolopale
cyt.	cytoplasmic parts of connective tissue cells	*sc.s.*	scolopale space
		sep.	transverse septa between cell membranes
d.p.	distal process of sensory cell		
d.pr.	distal prolongation of scolopale cell	*sh.*	sheath cell
enc.	scolopale cell enclave	*t.*	tube
env.	enveloping portion of scolopale cell	*t.s.*	terminal segment
eph.	ephapse	*v.*	vacuole in wall of tube

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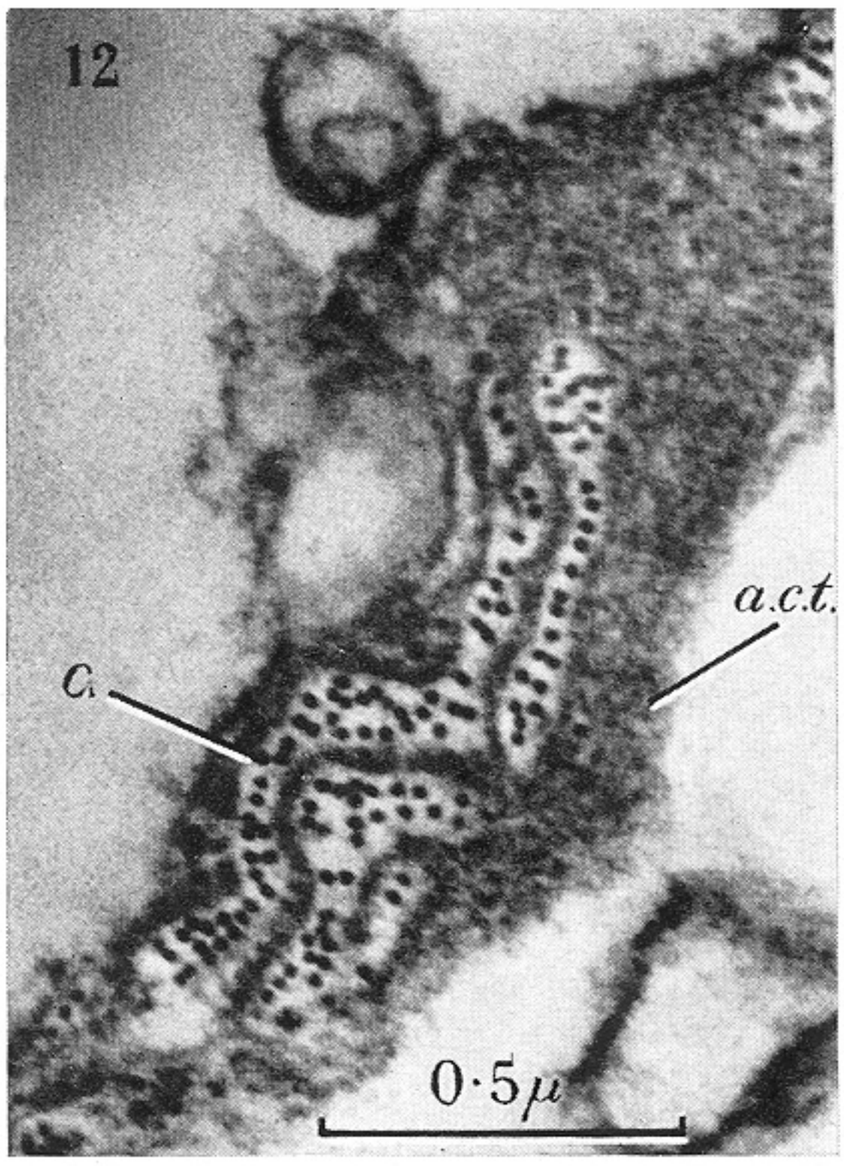

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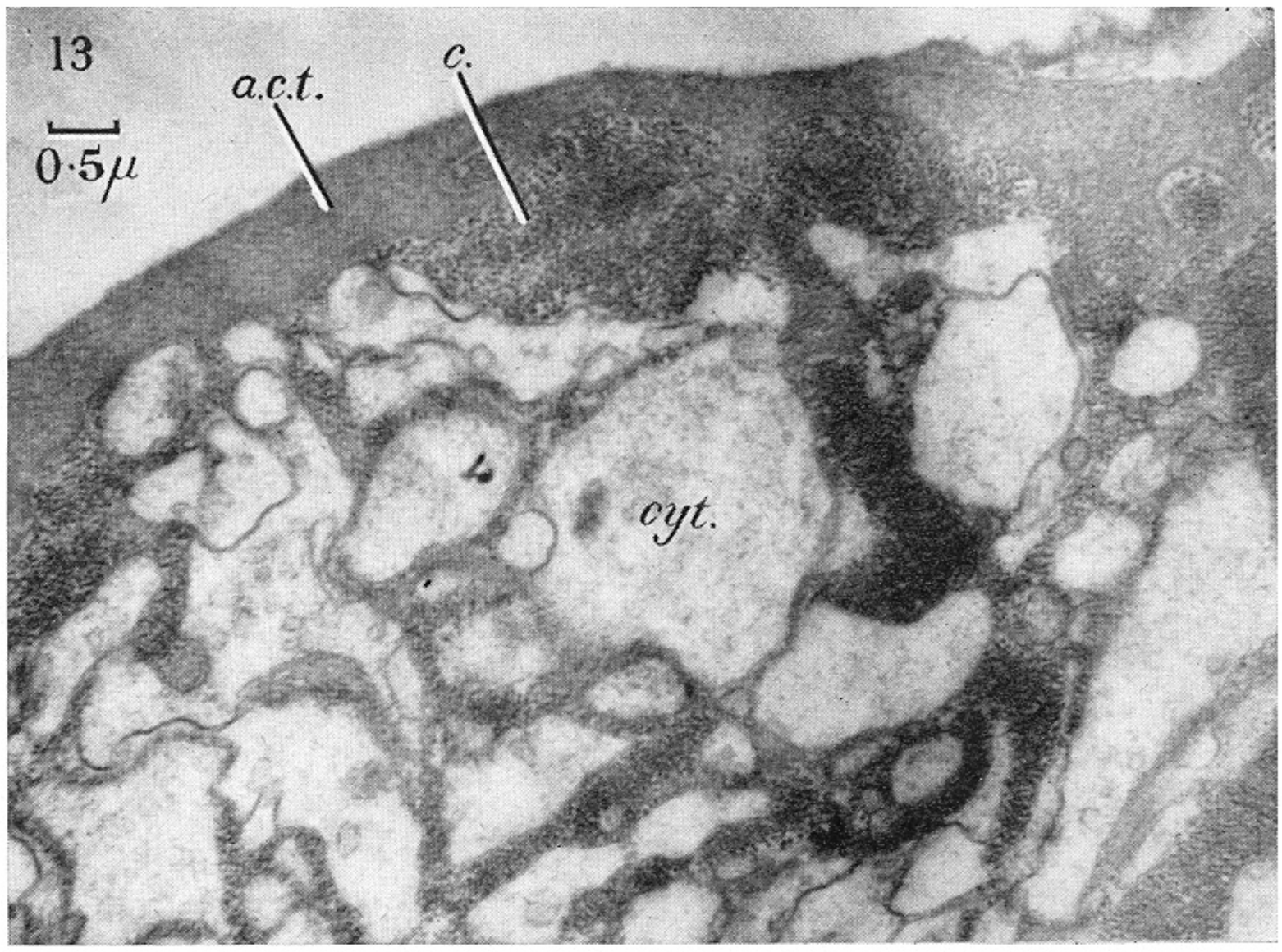

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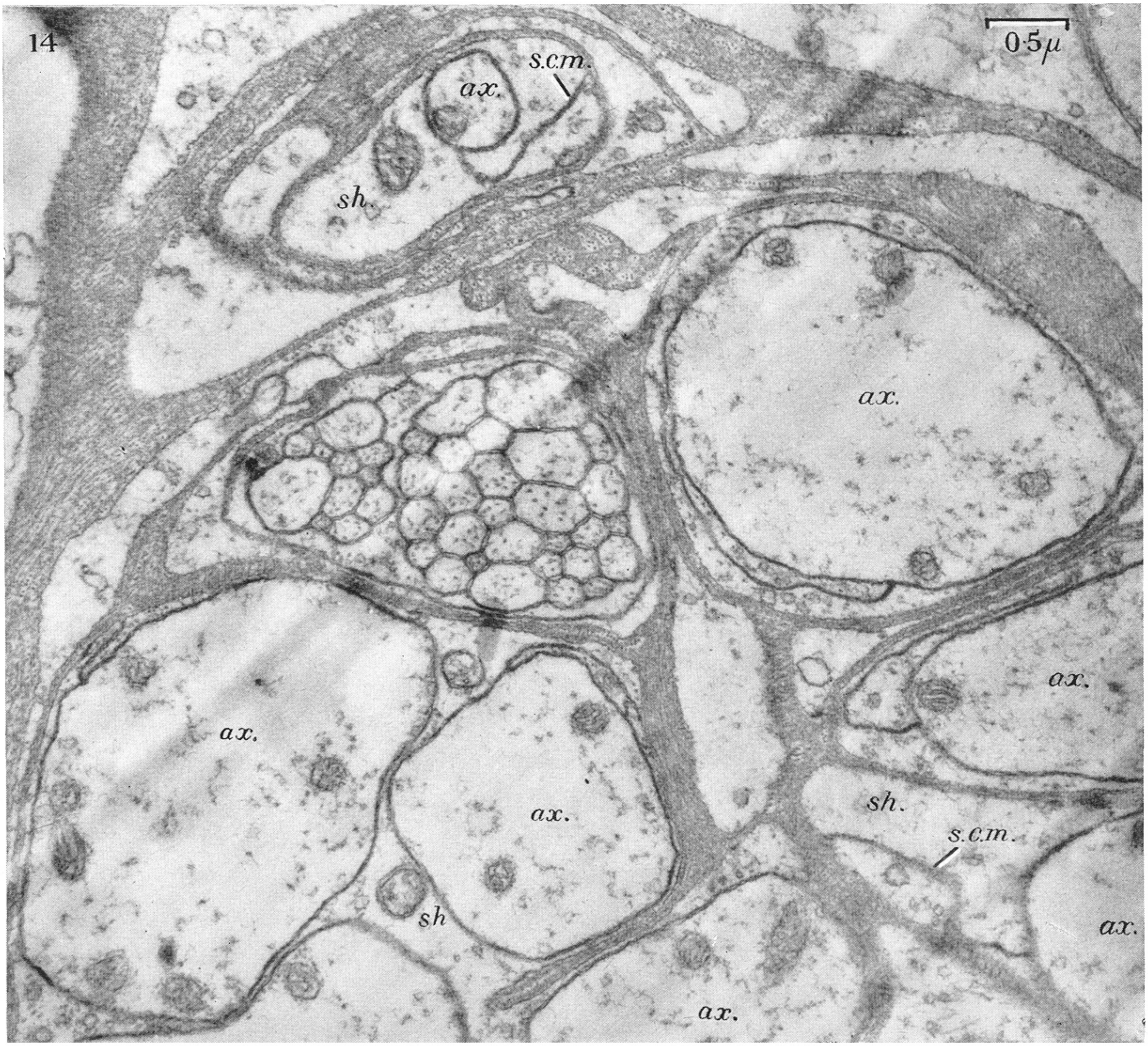

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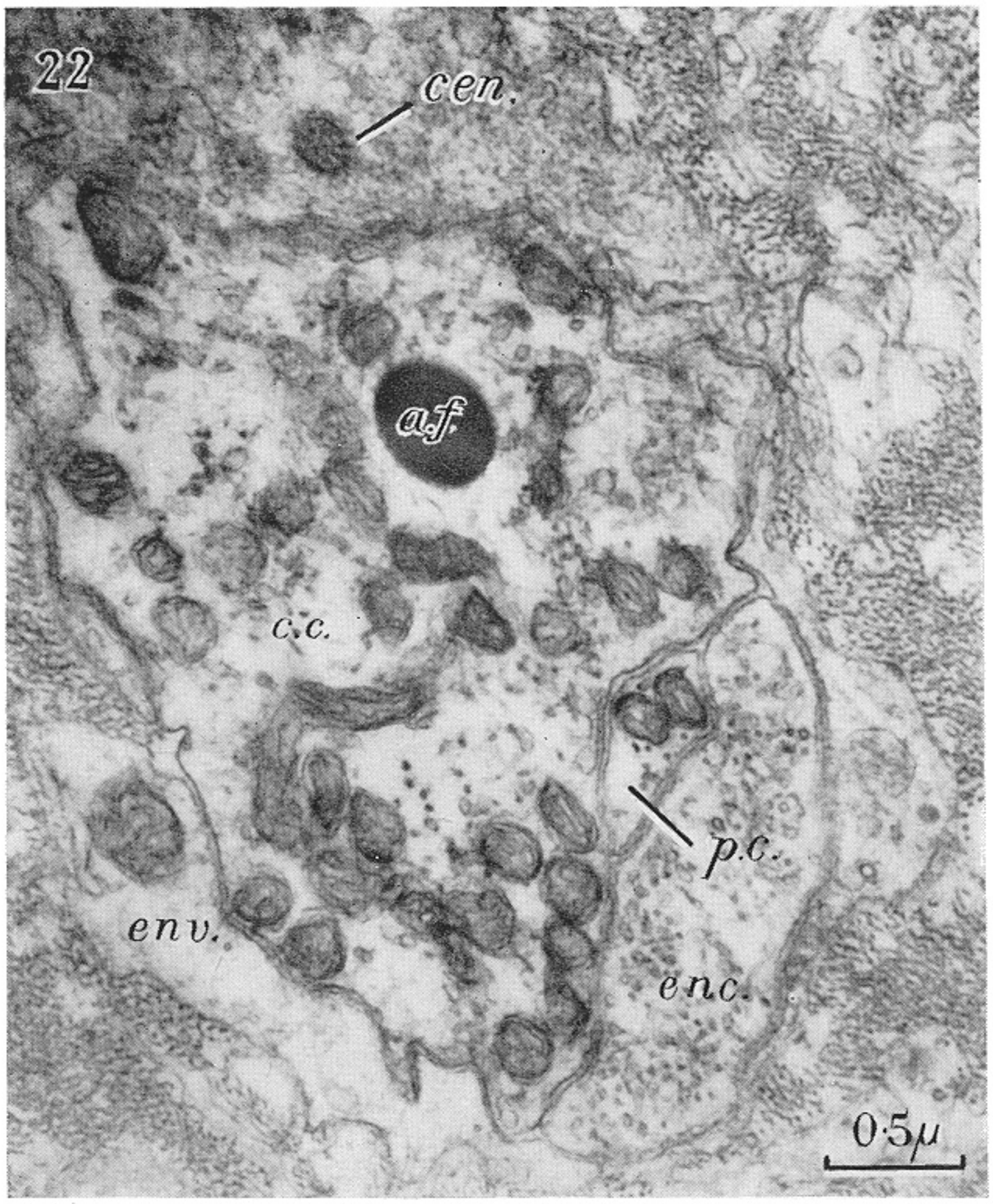

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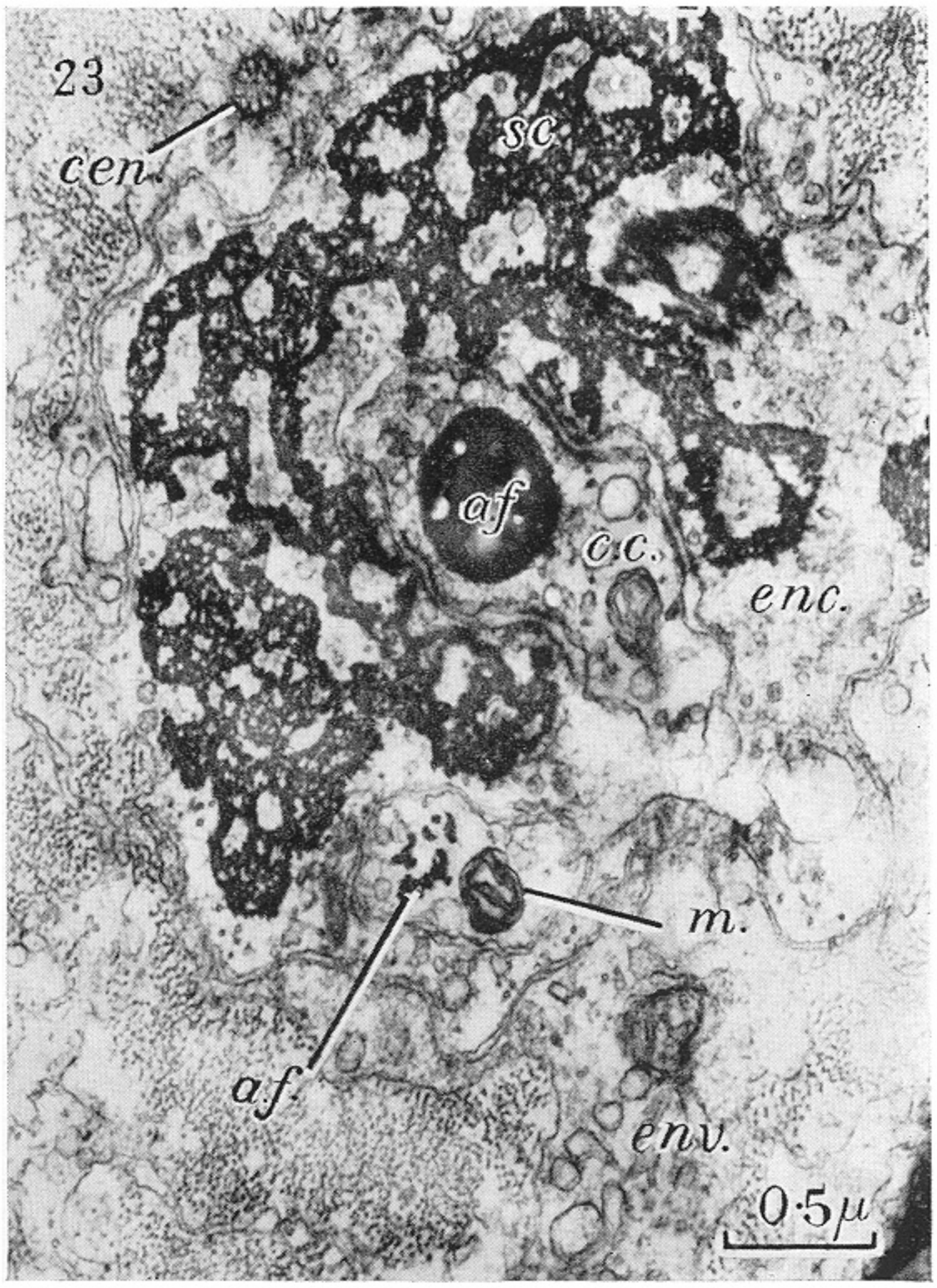

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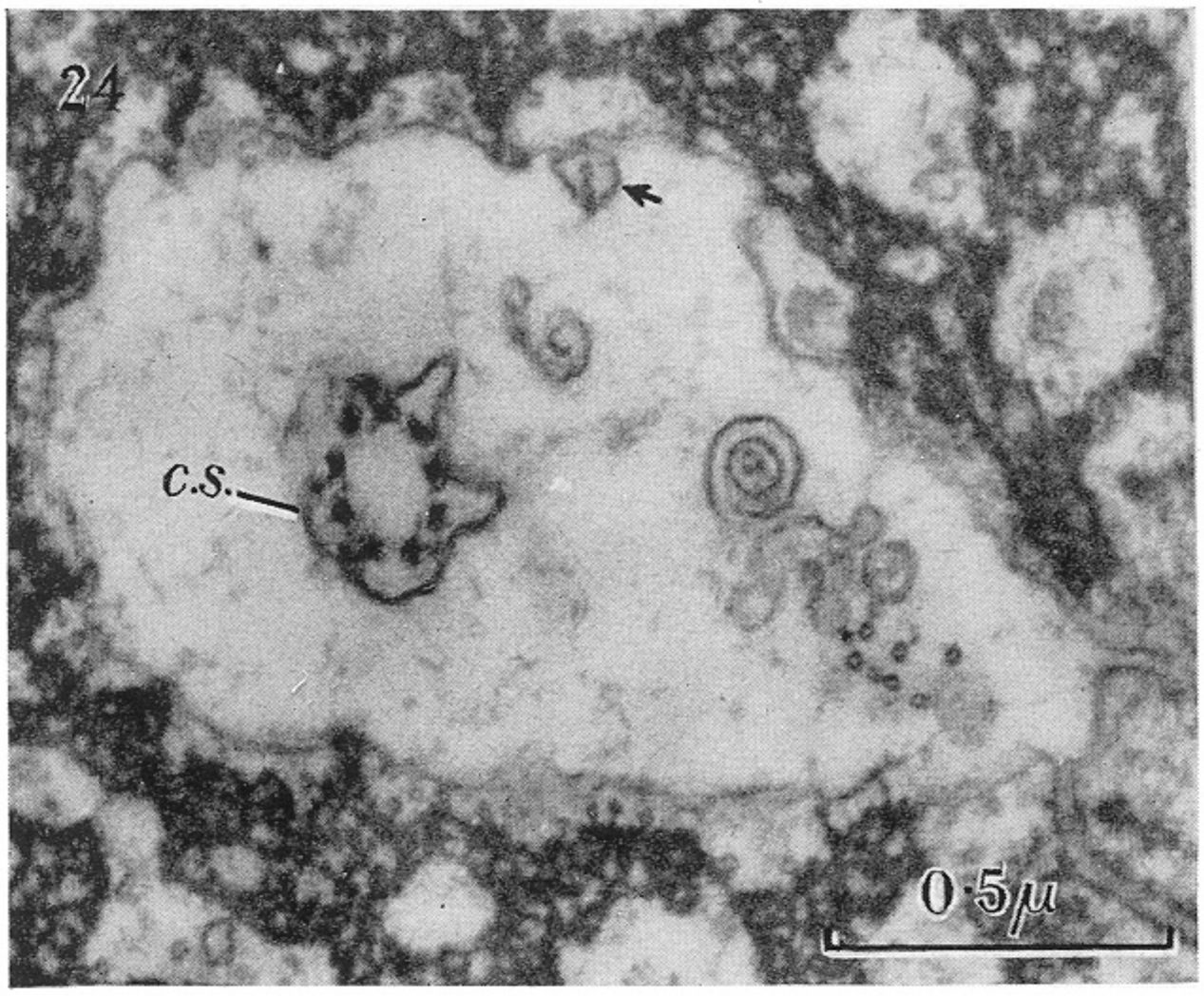

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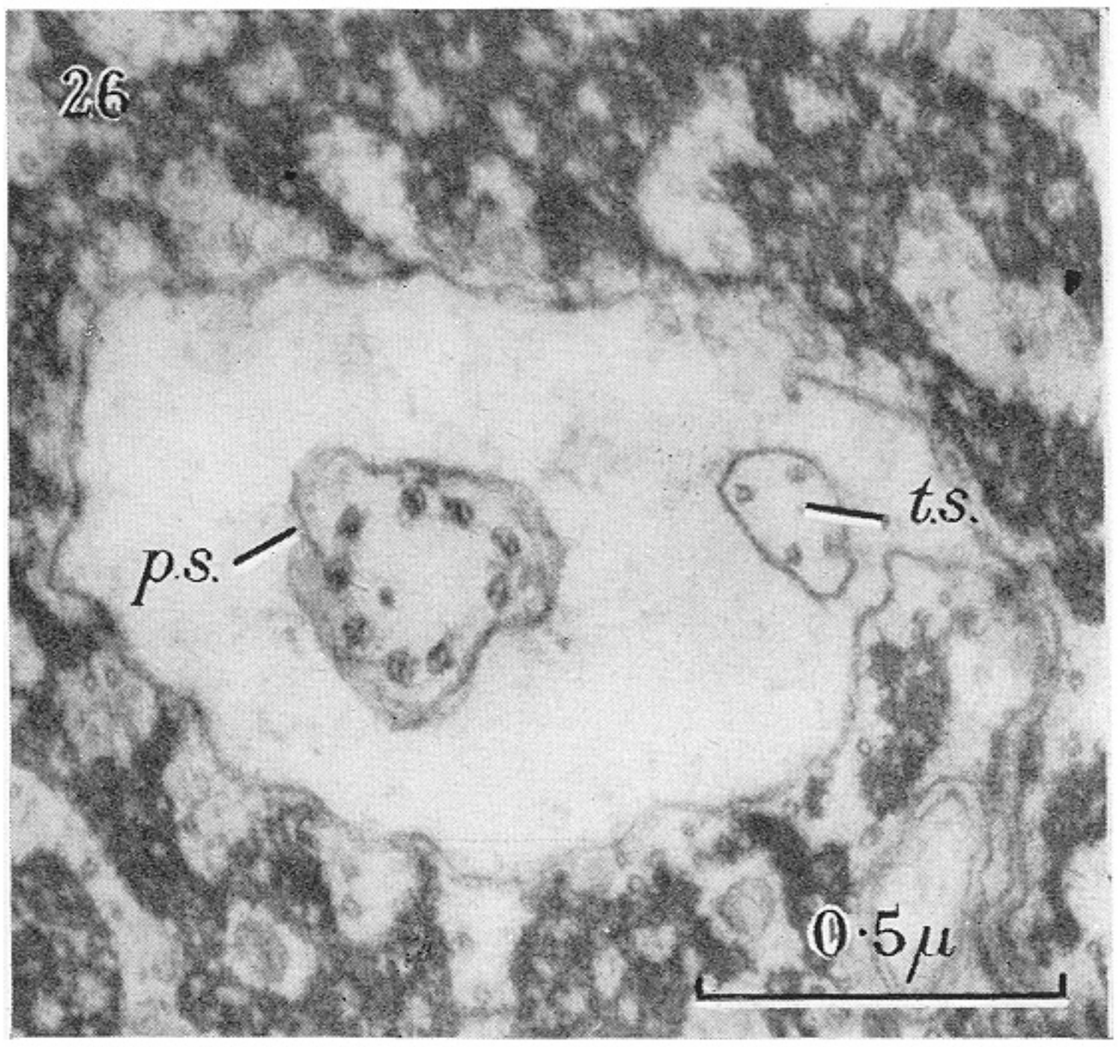

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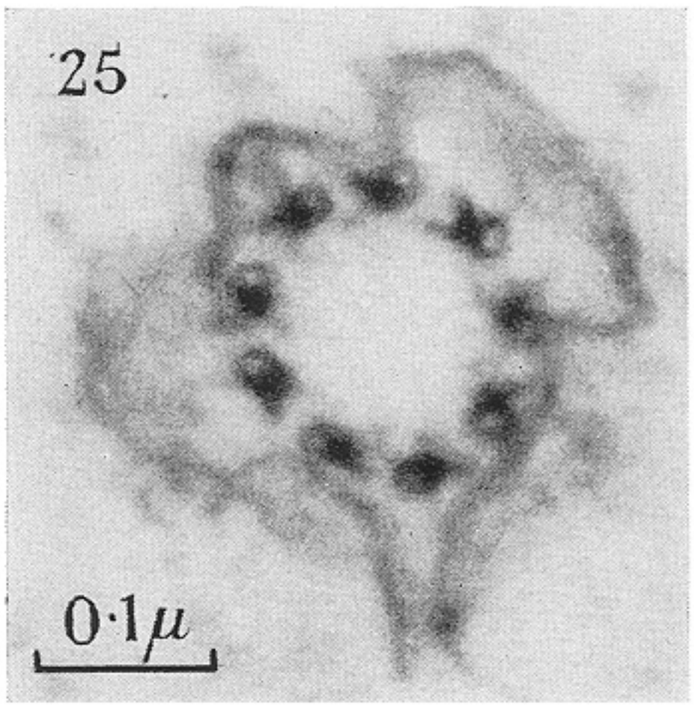

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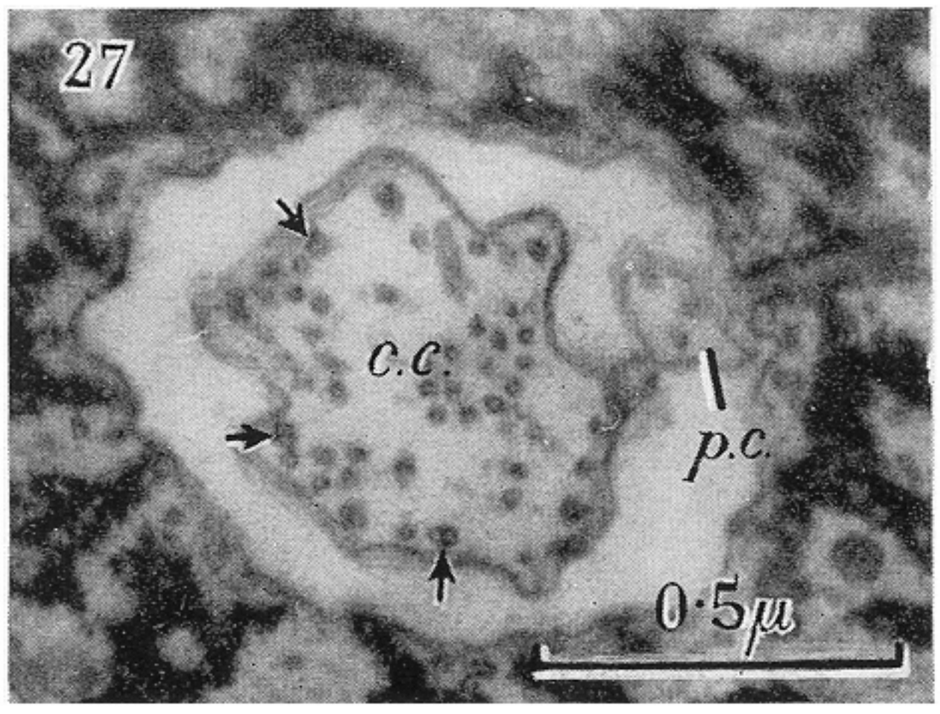

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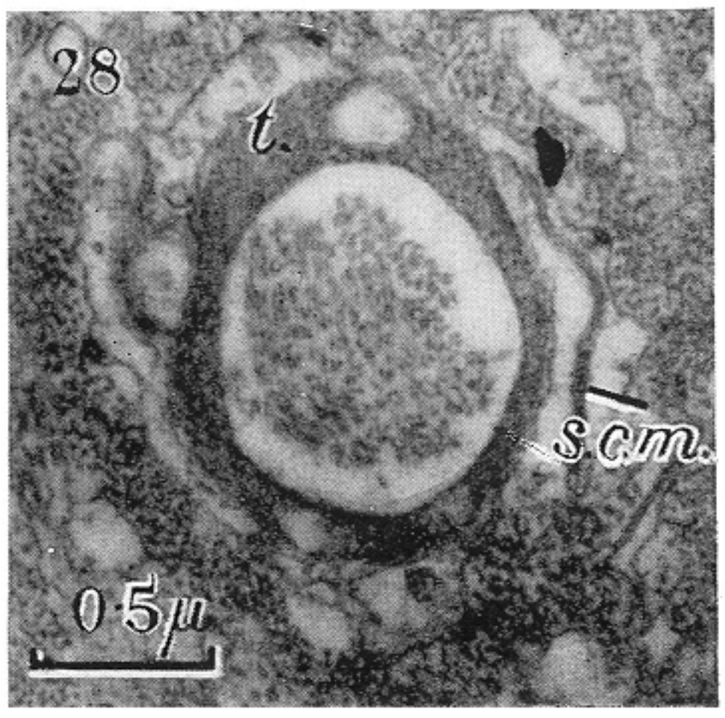

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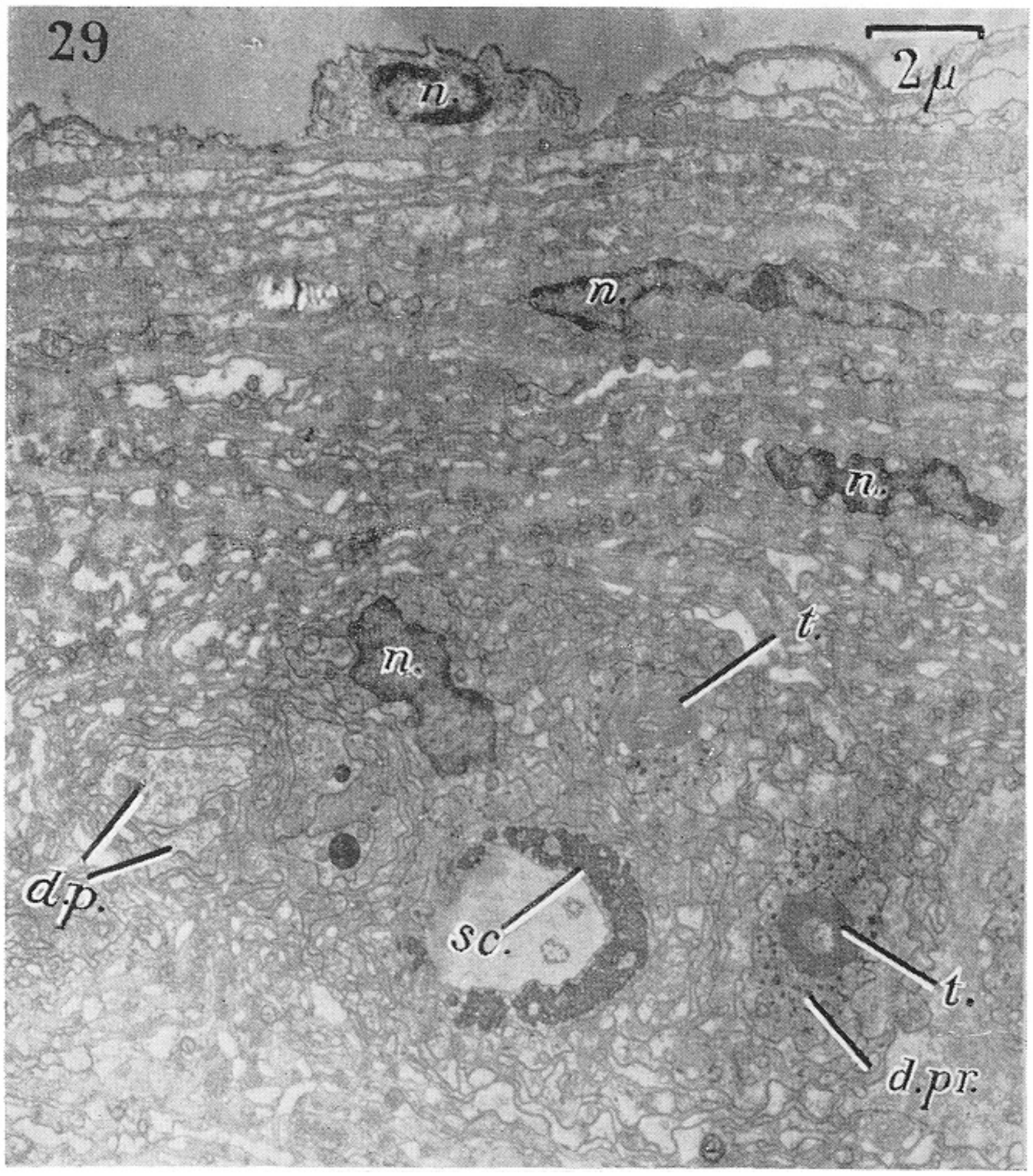
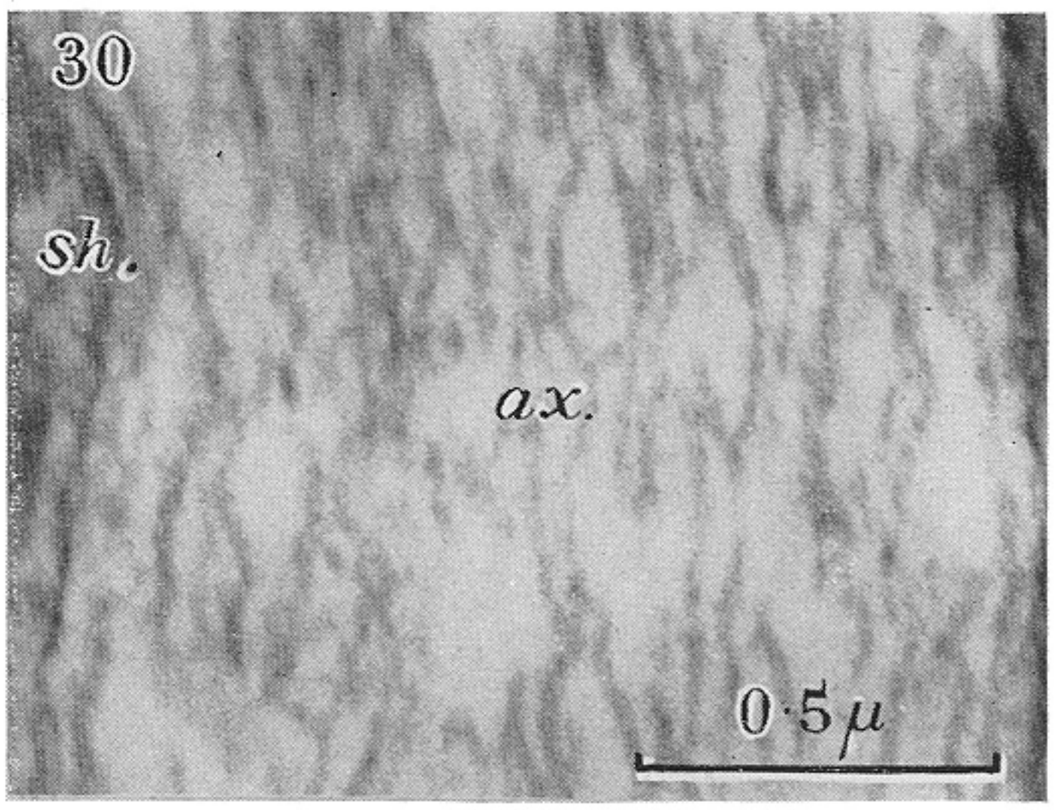
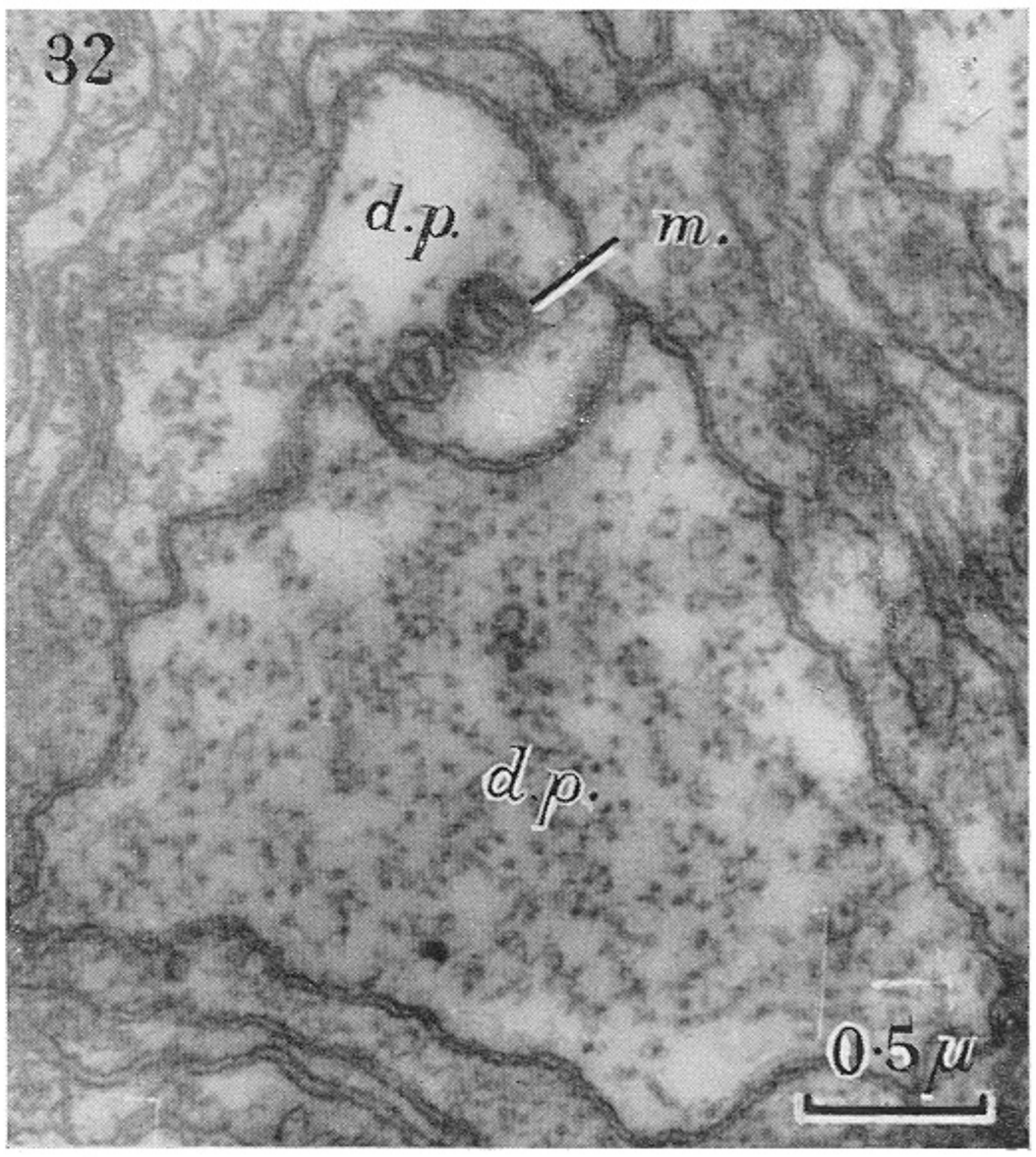

2μ
n.
n.
n.
n.
t.
d.p.
sc.
t.
d.pr.

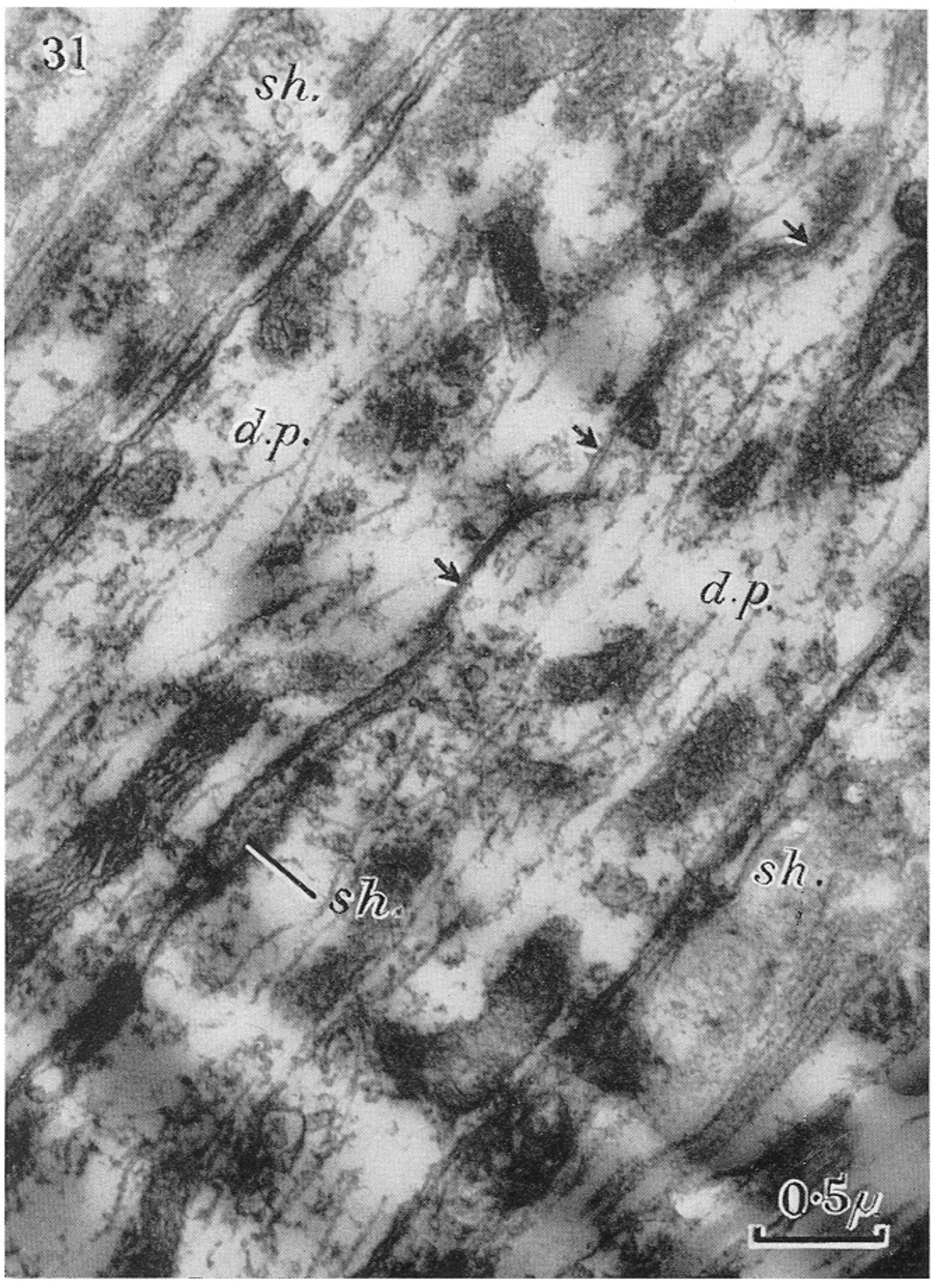
30


sh.
ax.
0·5μ

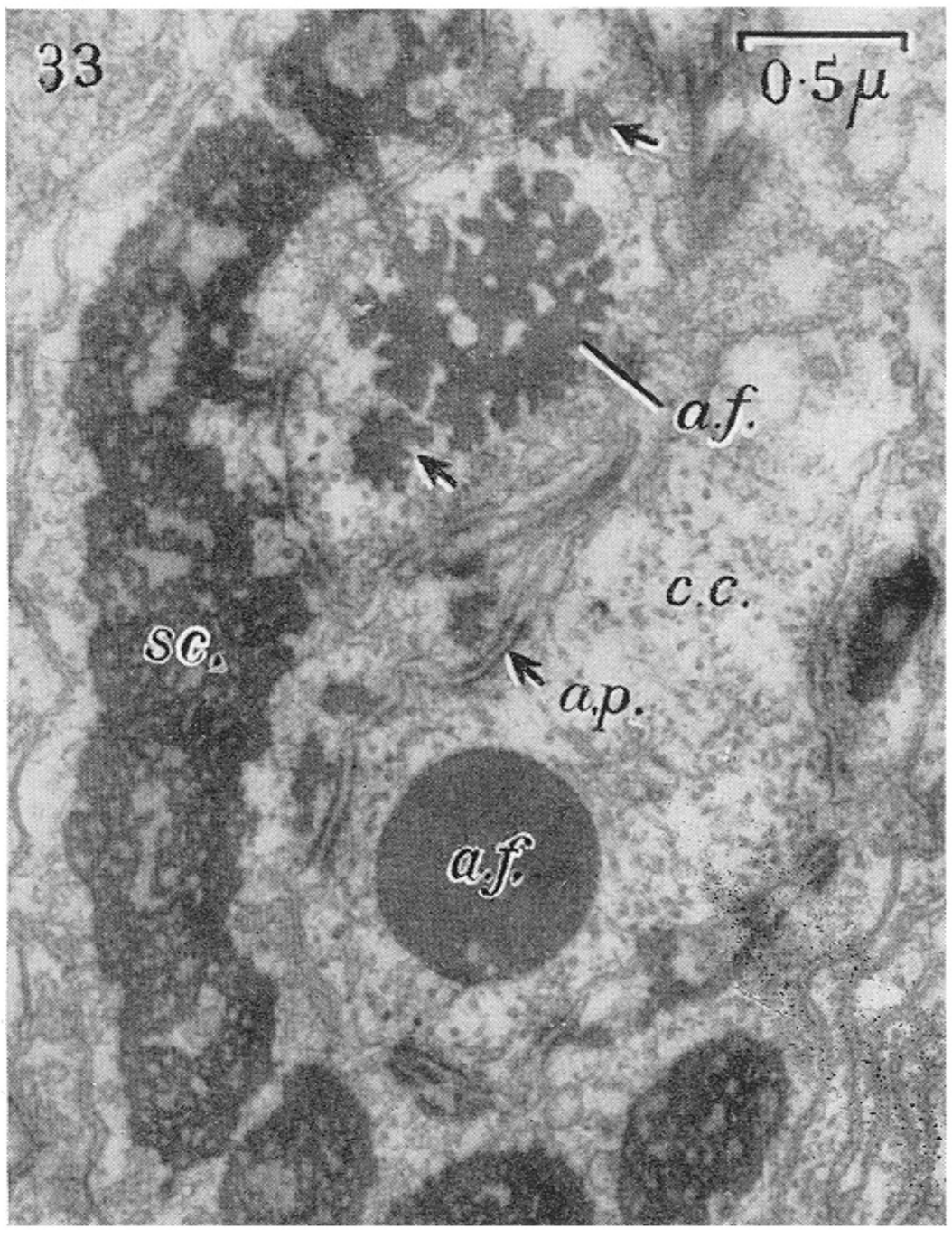
32


d.p.
m.
d.p.
0·5μ

31


sh.
d.p.
d.p.
sh.
sh.
0·5μ

33


0·5μ
a.f.
c.c.
sc.
a.p.
a.f.

34

0·5μ

c.s.

p.s.

35

c.s.

p.s.

0·5μ

36

0·5μ

env.

enc.

f.

t.s.

n.

37

t.

0·5μ

t.s.

d.pr.

d.pr.

38

d.pr.

can.c.

g.

d.pr.

0·5μ

39

can.c.

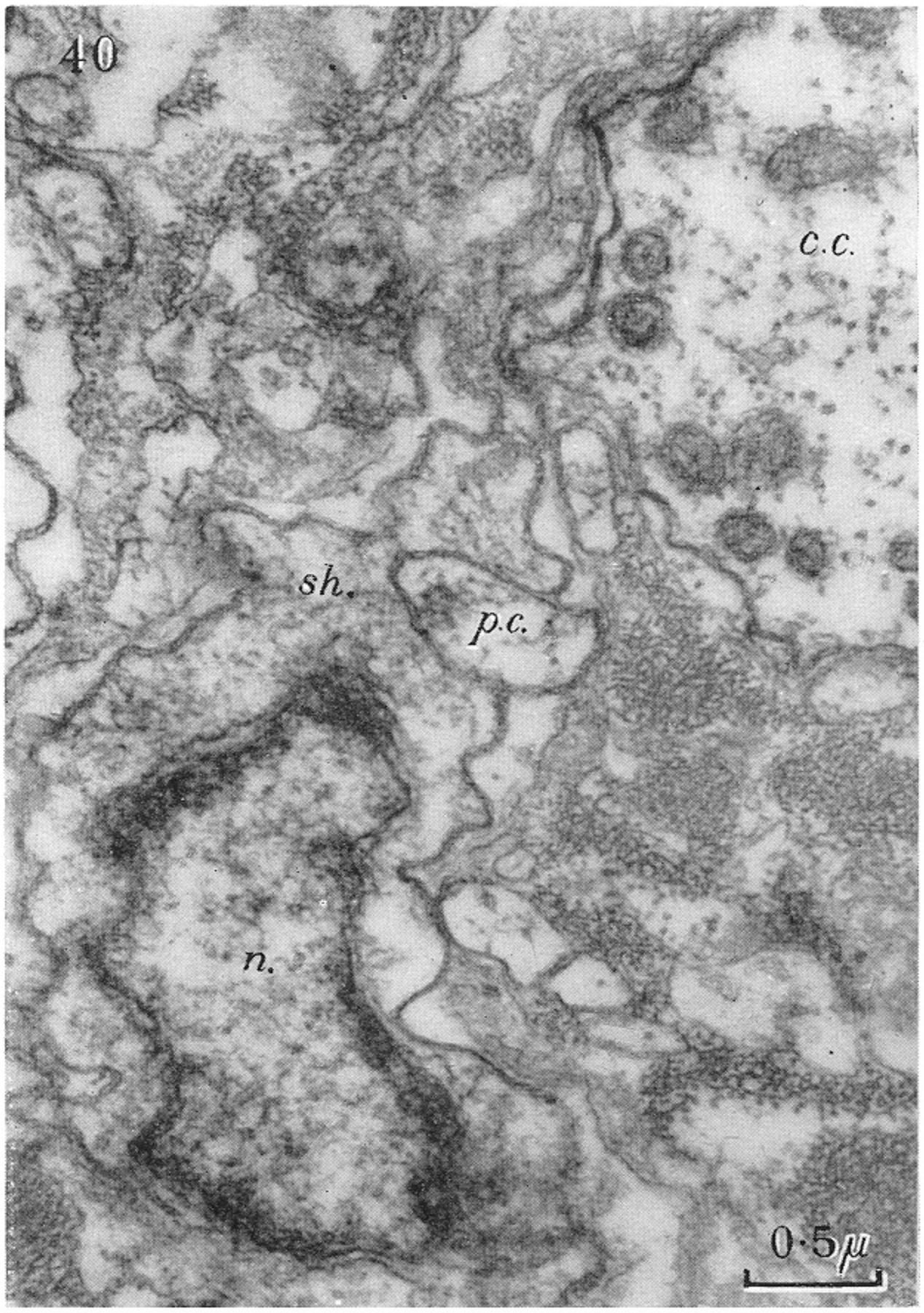
n.

t.

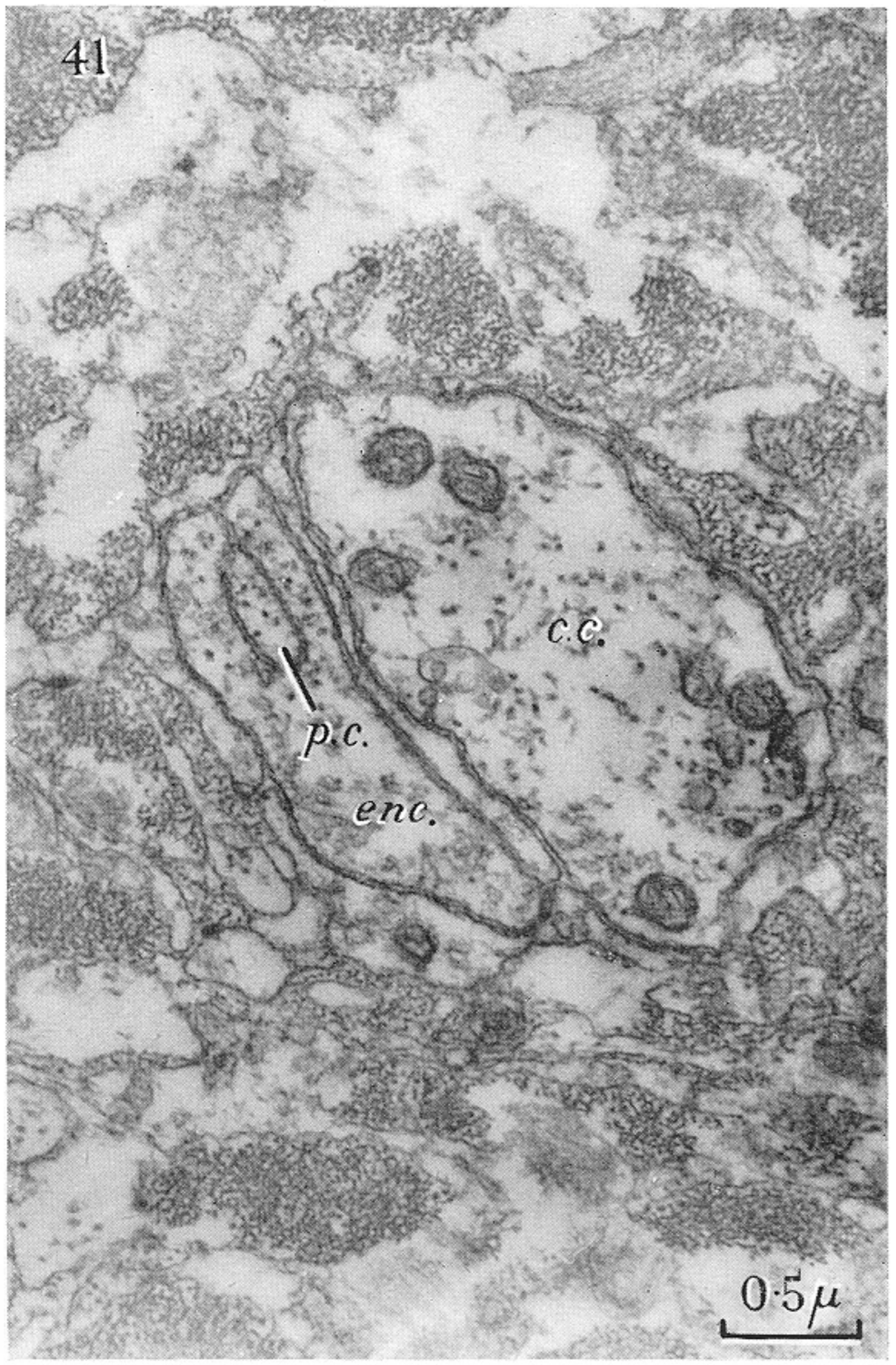
sep.

0·5μ

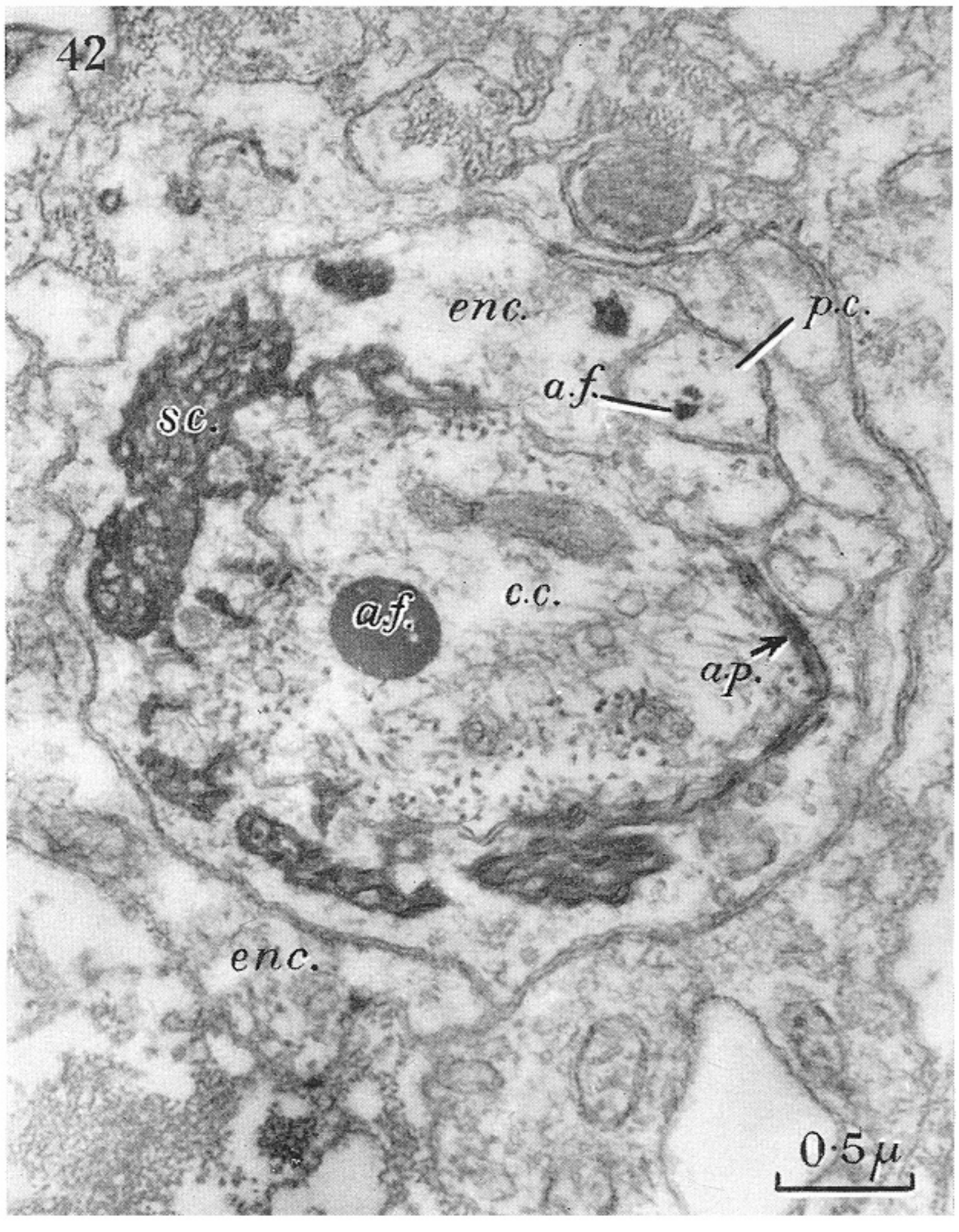
40


c.c.
sh.
p.c.
n.
0·5μ

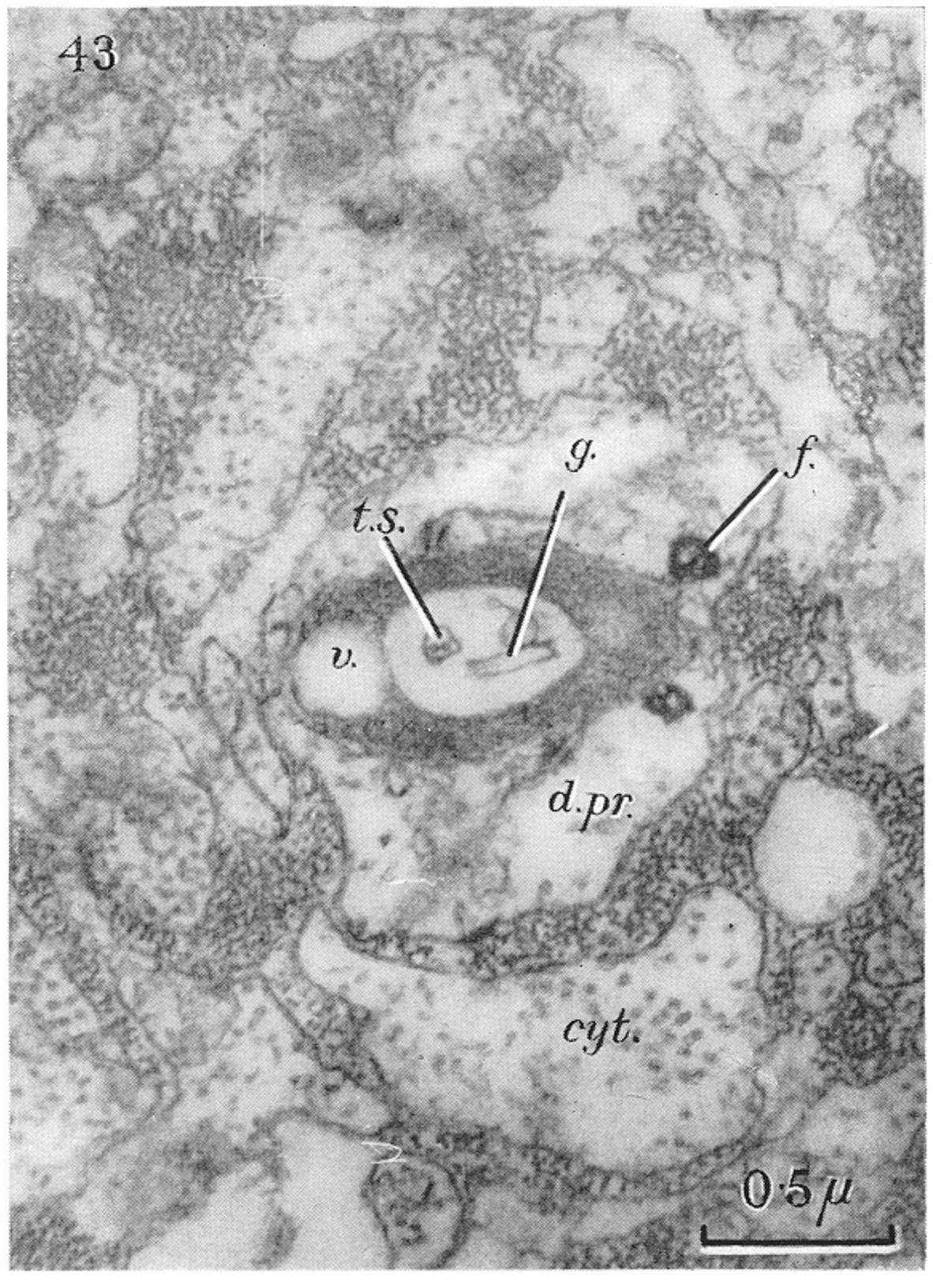
41


c.c.
p.c.
enc.
0·5μ

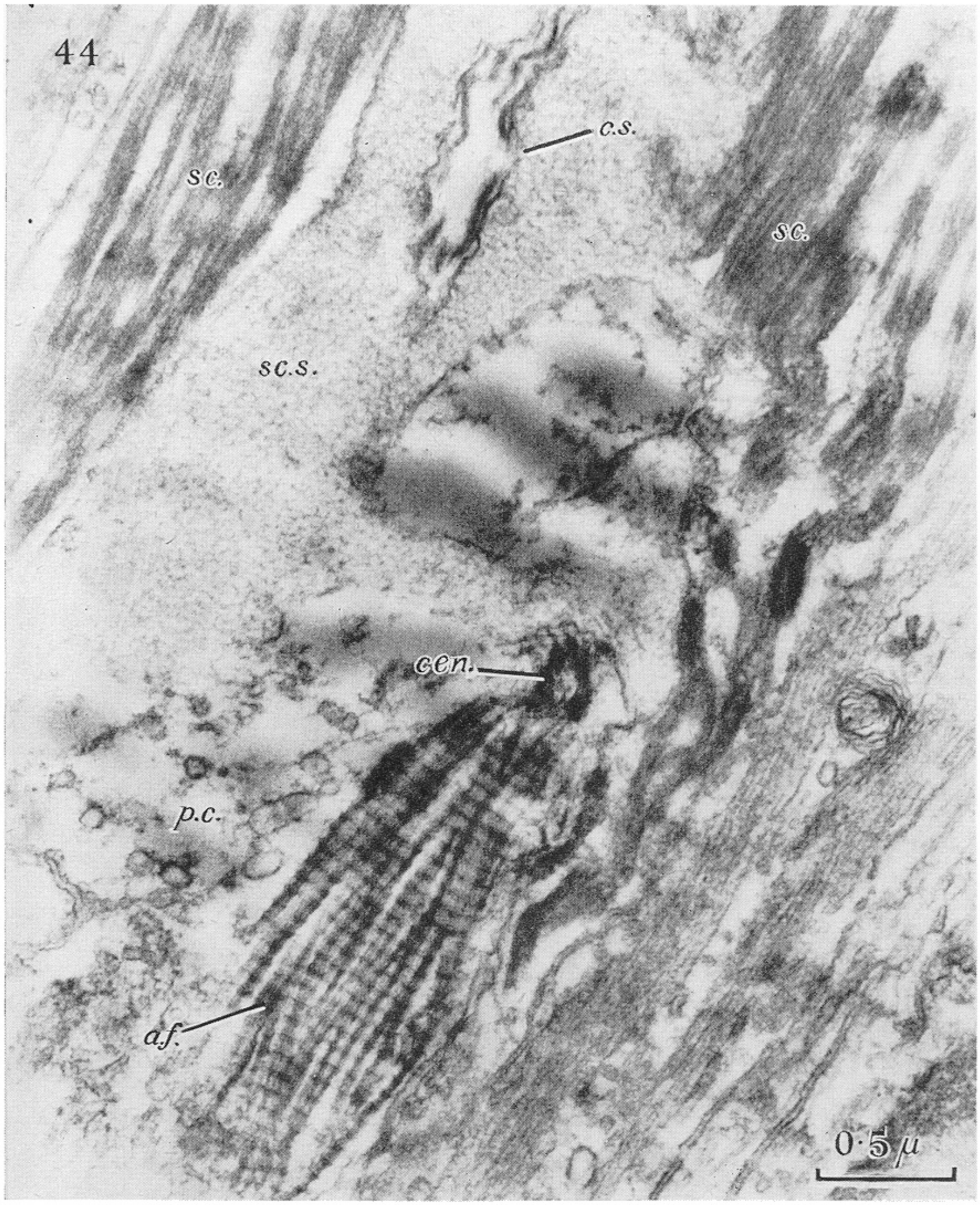
42


enc.
p.c.
a.f.
s.c.
c.c.
a.f.
a.p.
enc.
0·5μ

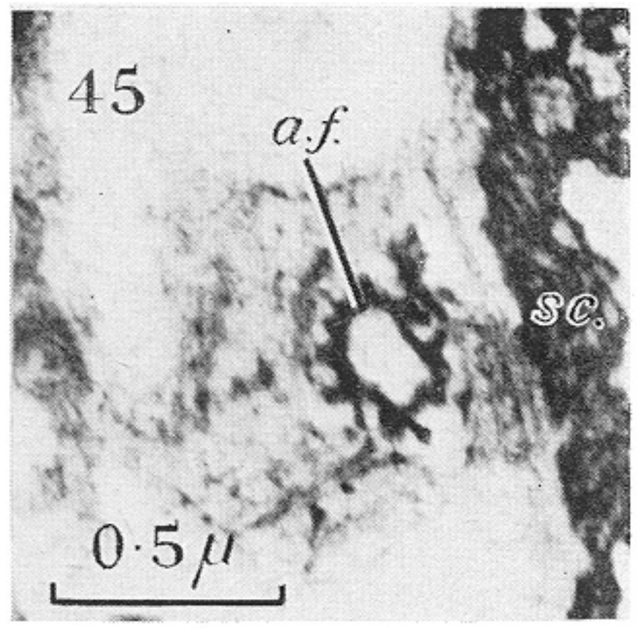
43


t.s.
g.
f.
v.
d.pr.
cyt.
0·5μ

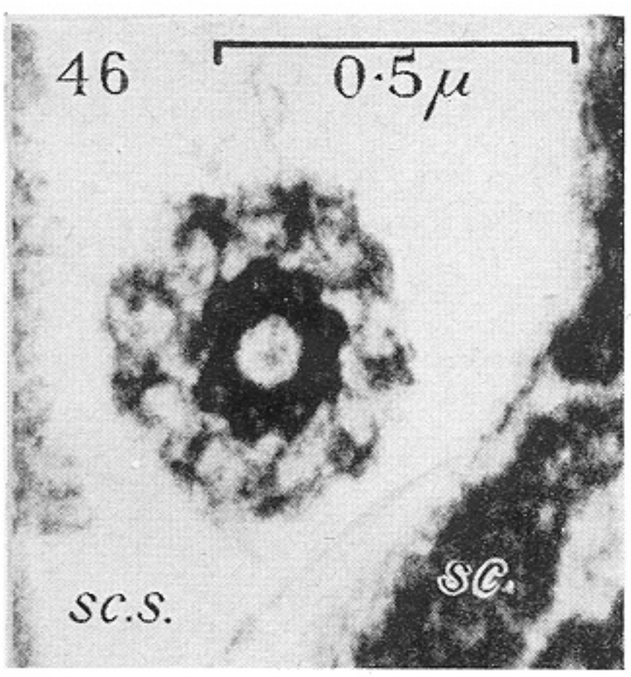
44



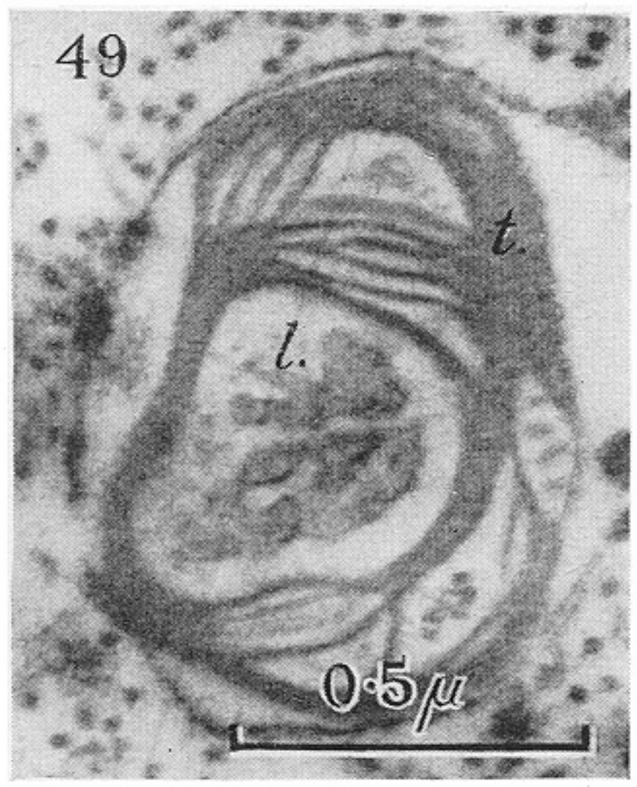
45



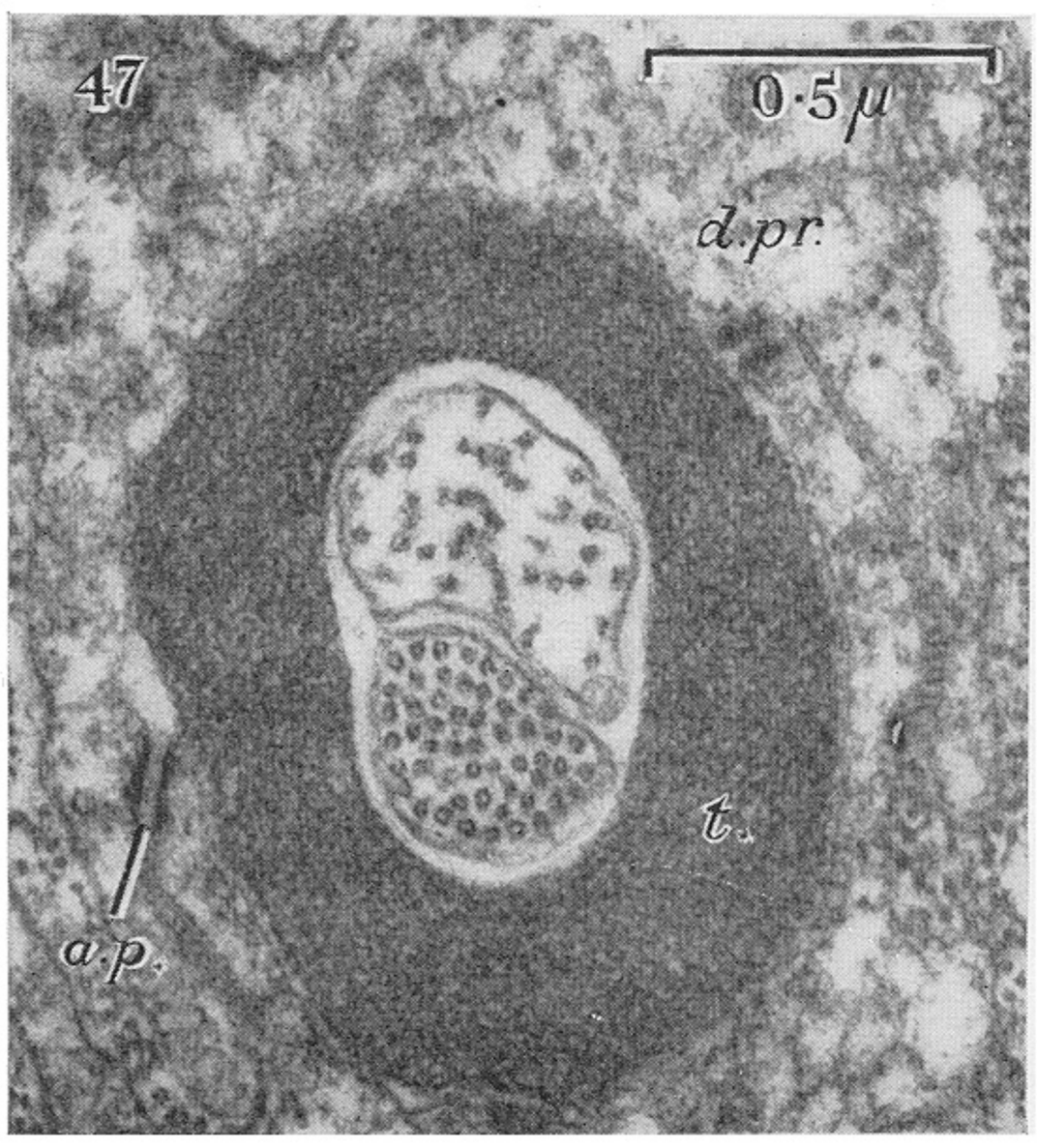
46



49



47



48